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# A review of toxoplasmosis in wild birds

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## Abstract

*Toxoplasma gondii* affects most species of warm-blooded animals, including birds. There is considerable confusion regarding the identity of *T. gondii*-like parasites and the diagnosis of toxoplasmosis in wild birds. In this review, *T. gondii*-like infections in different species of wild birds are reviewed with particular reference to prevalences, clinical signs, pathology, diagnosis, and treatment. Although subclinical *T. gondii* infections are prevalent in many avian species, toxoplasmosis can be clinically severe in pigeons and canaries. Blindness associated with *T. gondii* in canaries is reviewed in detail. © 2002 Elsevier Science B.V. All rights reserved.

**Keywords:** *Toxoplasma gondii*; Toxoplasmosis; Birds; Prevalence; Clinical signs; Diagnosis; Treatment

## 1. History

*Toxoplasma*-like parasites were observed by Carini (1911) in smears prepared from the liver and spleen of a pigeon in São Paulo, Brazil. Previously, there were reports of *Toxoplasma*-like parasites in sparrows and other birds, but they were considered hemoprotozoans (Laveran, 1900; Adie, 1908; Aragão, 1911). Subsequently, such parasites were reported from several species of birds (Laveran and Marullaz, 1913; Marullaz, 1913; Plimmer, 1915, 1916; de Mello, 1915, 1935; Raffaele, 1932; Herman, 1937; Hegner and Wolfson, 1938a,b; Taddia, 1938; Taddia and Valentino, 1939). All of these reports were based on findings of *Toxoplasma*-like organisms in blood smears or tissue imprints of liver and spleen. In retrospect, there is no way to ascertain the identity of these organisms. Because sparrows are host to other apicomplexans (Baker et al., 1972; Levine, 1982), the parasites in these reports were probably misdiagnosed as *Toxoplasma*. In several papers, *Toxoplasma*-like parasites from birds were given different names, *T. avium* (Marullaz, 1913), *T. francae*,

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*T. fulicae* (de Mello, 1915, 1935), and *T. columbae* (Yakimoff and Kohl-Yakimoff, 1912), but Levine (1977) synonymized all avian *Toxoplasma* species with *Toxoplasma gondii*.

Reis and Nóbrega (1936) and Nóbrega and Reis (1942) isolated *T. gondii* from pigeons and transmitted them to other animals. From 1941 to 1960, research interest in *Toxoplasma* infections in birds increased in part because researchers sought to determine if avian *Toxoplasma* was identical with mammalian *Toxoplasma*, whether the higher body temperature of birds (41 °C) in comparison to mammals (37 °C) had any effect on *T. gondii*, and whether birds were a possible source of *T. gondii* infection in humans (Wolfson, 1941; Manwell, 1941; Manwell et al., 1945; Manwell and Drobeck, 1951; Drobeck et al., 1953; Jacobs et al., 1952, 1953; Feldman and Sabin, 1949). The finding of *T. gondii* in nucleated avian erythrocytes (Fig. 1) was also of biologic interest because *T. gondii* is not found in non-nucleated mammalian cells (Manwell, 1941; Wolfson, 1941).

The development of a reliable serologic test (the dye test) by Sabin and Feldman (1948) made it possible to serologically compare assumed *T. gondii* infection from various animal species. In the 1950s and 1960s, it became clear that there were no morphologic or serologic differences among various isolates of *T. gondii* from avian or mammalian hosts. As a result of serologic and parasitologic surveys, it became clear that *T. gondii* infection was common in some avian species (Tables 1 and 2).

It is not possible to list in this review all species of birds that have been reported as hosts of *T. gondii*. Coutelen et al. (1953), Drobeck et al. (1953), and Siim et al. (1963)

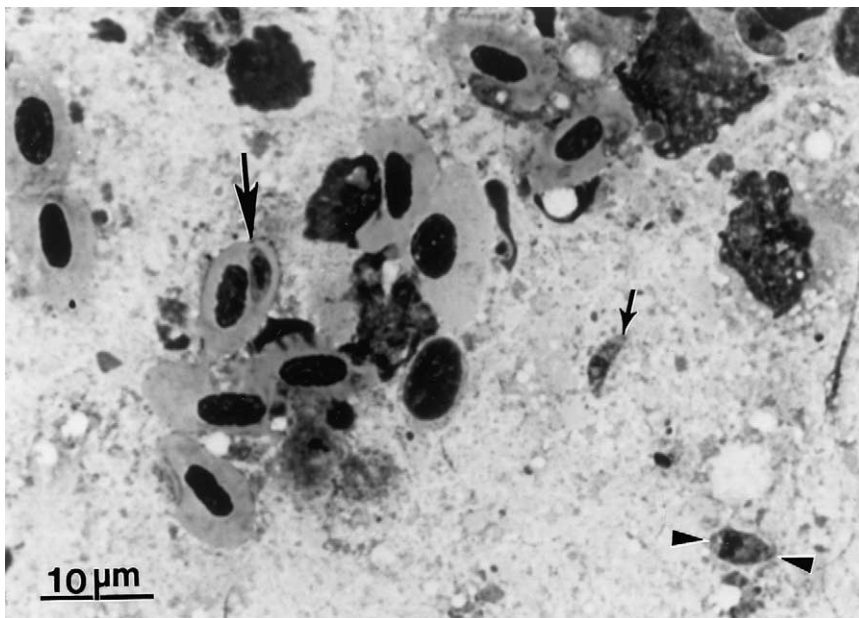


Fig. 1. *Toxoplasma gondii* tachyzoites inside an erythrocyte (large arrow), outside of cells (small arrow) and a dividing tachyzoite (arrowheads) in impression smear of small intestine of an experimentally-infected budgerigar (Giemsa).

Table 1

Isolation of *Toxoplasma gondii* from tissues of naturally-infected wild birds

Species	Country	No. bioassayed	Infected (%)	Reference
Anseriformes (wildfowl, ducks)				
Mallard ( <i>Anas platyrhynchos</i> )	Czech Republic	184	12.0	Literák et al. (1992)
Pochard ( <i>Aythya ferrina</i> )	Czech Republic	8	12.5	Literák et al. (1992)
Tufted duck ( <i>Aythya fuligula</i> )	Czech Republic	25	28.0	Literák et al. (1992)
Pintail ( <i>Anas acuta</i> )	Kazakhstan	57	1.8	Pak (1976)
Gadwall ( <i>Anas strepera</i> )	Kazakhstan	93	1.1	Pak (1976)
Accipitriformes (harriers, hawks, vultures, buzzards, kestrels)				
Goshawk ( <i>Accipiter gentilis</i> )	Czech Republic	10	10.0	Literák et al. (1992)
Cooper's hawk ( <i>Accipiter cooperi</i> )	USA	4	25	Lindsay et al. (1993)
Common buzzard ( <i>Buteo buteo</i> )	Czech Republic	123	8.1	Literák et al. (1992)
	Kazakhstan	12	8.3	Pak (1976)
Kestrel ( <i>Falco tinnunculus</i> )	Czech Republic	1	100	Literák et al. (1992)
American kestrel ( <i>Falco sparverius</i> )	USA	3	33.3	Lindsay et al. (1993)
Pallid harrier ( <i>Circus macrourus</i> )	Kazakhstan	3	33.3	Pak (1976)
Black vulture ( <i>Aegypius monachus</i> )	Kazakhstan	4	25.0	Pak (1976)
Red-tailed hawk ( <i>Buteo jamaicensis</i> )	USA	27	41.1	Lindsay et al. (1993)
Red-shouldered hawk ( <i>Buteo lineatus</i> )	USA	12	66.7	Lindsay et al. (1993)
Galliformes (partridges, pheasants, turkeys)				
Partridge ( <i>Perdix perdix</i> )	Czech Republic	16	18.7	Literák et al. (1992)
Pheasant ( <i>Phasianus colchicus</i> )	Czech Republic	590	2.4	Literák et al. (1992)
	Slovakia	1	100	Čatár (1974)
Turkey ( <i>Meleagris gallopavo</i> )	USA	16	50	Lindsay et al. (1994)
Gruiformes (coots)				
Coot ( <i>Fulica atra</i> )	Czech Republic	43	4.6	Literák et al. (1992)
	Kazakhstan	29	3.4	Pak (1976)
Charadriiformes (gulls, terns)				
Blackheaded gull ( <i>Larus ridibundus</i> )	Czech Republic	61	16.4	Literák et al. (1992)
	Kazakhstan	84	1.2	Pak (1976)
Common tern ( <i>Sterna hirundo</i> )	Kazakhstan	14	7.1	Pak (1976)
	USSR	3	33.3	Pak (1970)
Columbiformes (pigeons, doves)				
Collared dove ( <i>Streptopelia decaocto</i> )	Czech Republic	60	5.0	Literák et al. (1992)
	Slovakia	12	50	Čatár (1974)
Woodpigeon ( <i>Columba palumbus</i> )	Czech Republic	12	8.3	Literák et al. (1992)

Table 1 (Continued)

Species	Country	No. bioassayed	Infected (%)	Reference
Rock dove common pigeon ( <i>Columba livia</i> )	Czech Republic	606	1.0	Literák et al. (1992)
	Denmark	3	100	Siim et al. (1963)
	Slovakia	16	12.5	Čatár (1974)
	USA	1	100	Feldman and Sabin (1949)
	USA	50	2	Manwell and Drobeck (1951)
	USA	80	5	Jacobs et al. (1952)
	USA	16	6	Gibson and Eyles (1957)
Laughing dove ( <i>Streptopelia senegalensis</i> )	Kazakhstan	20	5.0	Pak (1976)
Ruddy-ground dove ( <i>Columbina talpacoti</i> )	Panama	79	3	Frenkel et al. (1995)
Strigiformes (owls)				
Ferruginous pygmy owl ( <i>Glaucidium brasilianum</i> )	Costa Rica	1	Not given	Holst and Chinchilla (1990)
Little owl ( <i>Athene noctua</i> )	Kazakhstan	15	6.7	Pak (1976)
Great horned owl ( <i>Bubo virginianus</i> )	USA	5	20	Lindsay et al. (1993)
Barred owl ( <i>Strix varia</i> )	USA	15	26.7	Lindsay et al. (1993)
Passeriformes (various passerine birds)				
Great grey shrike ( <i>Lanius excubitor</i> )	Czech Republic	1	100	Literák et al. (1992)
Yellowhammer ( <i>Emberiza citrinella</i> )	Czech Republic	5	20	Hejlíček et al. (1981)
Chaffinch ( <i>Fringilla coelebs</i> )	Czech Republic	185	0.5	Literák et al. (1992)
	Czech Republic	133	0.7	Literák et al. (1992)
	Czech Republic	152	0.7	Literák et al. (1992)
House sparrow ( <i>Passer domesticus</i> )	Costa Rica	106	16	Ruiz and Frenkel (1980)
	Czech Republic	1907	0.5	Literák et al. (1992)
	Czech Republic	40	17.5	Hejlíček et al. (1981)
	Kazakhstan	177	1.7	Pak (1976)
	Slovakia	5	40	Čatár (1974)
Tree sparrow ( <i>Passer montanus</i> )	USSR	412	0.5	Pak (1972)
	Czech Republic	4	25	Hejlíček et al. (1981)
	Czech Republic	316	0.6	Literák et al. (1992)
	Kazakhstan	178	0.6	Pak (1976)
Jay ( <i>Garrulus glandarius</i> )	Czech Republic	43	2.3	Literák et al. (1992)
Starling ( <i>Sturnus vulgaris</i> )	Czech Republic	69	1.4	Literák et al. (1992)
Palm tanager ( <i>Thraupis palmarum</i> )	Kazakhstan	430	0.5	Pak (1976)
	Panama	3	33.3	Frenkel et al. (1995)
Black bird ( <i>Turdus merula</i> )	Czech Republic	54	1.9	Literák et al. (1992)
	Slovakia	4	25	Čatár (1974)

Table 1 (Continued)

Species	Country	No. bioassayed	Infected (%)	Reference
Mistle thrush ( <i>Turdus viscivorus</i> )	Slovakia	1	100	Čatár (1974)
Song thrush ( <i>Turdus philomelos</i> )	Slovakia	7	71.4	Čatár (1974)
Robin ( <i>Erithacus rubecula</i> )	Slovakia	8	37.5	Čatár (1974)
Great tit ( <i>Parus major</i> )	Czech Republic	215	1.4	Literák et al. (1992)
	Slovakia	5	40	Čatár (1974)
Nuthatch ( <i>Sitta europea</i> )	Slovakia	6	33	Čatár (1974)
Treecreeper ( <i>Certhia familiaris</i> )	Slovakia	1	100	Čatár (1974)
Greenfinch ( <i>Chloris chloris</i> )	Slovakia	1	100	Čatár (1974)
American crow ( <i>Corvus brachyrhynchos</i> )	USA	82	1.2	Finlay and Manwell (1956)
Carriion crow ( <i>Corvus corone</i> )	Kazakhstan	58	1.7	Pak (1976)
	Slovakia	4	50	Čatár (1974)
Jackdaw ( <i>Corvus monedula</i> )	Czech Republic	5	20.0	Literák et al. (1992)
Rook ( <i>Corvus frugilegus</i> )	Czech Republic	495	18.0	Literák et al. (1992)

have summarized earlier reports of *Toxoplasma*-like infections in birds. As stated earlier, in some of these reports, diagnosis may not have been accurate because there were no *T. gondii*-specific serologic or immunohistochemical techniques available prior to 1950. With respect to avian species, the only verified hosts of *T. gondii* are those from which *T. gondii* has been isolated by bioassays (Table 1).

## 2. Isolates of *T. gondii* from various avian species

Reports of isolation of viable *T. gondii* from tissues of various avian species without clinical signs are summarized in Table 1. Most of these reports are based on isolation of *T. gondii* from avian tissues bioassayed into mice.

## 3. Serologic prevalence

Serologic prevalence of *T. gondii* infections in different species of birds is summarized in Table 2, but not all surveys are listed. Caution should be used while interpreting the serologic prevalence data because not all serologic tests used in mammals work with avian sera. For example, the Sabin–Feldman dye test (DT) can detect antibodies in sera of pigeons but not in sparrows, chickens (Frenkel, 1981), and several other avian species (see section on serologic tests). For example, Ruiz and Frenkel (1980) isolated viable *T. gondii* from 16% of 106 sparrow without detectable DT antibodies.

In addition to Table 2, birds in zoological gardens in Czechoslovakia (Ippen et al., 1981), Korea (Choi et al., 1987), China (Zhang et al., 2000), and Japan (Murata, 1989) were found

Table 2  
Serologic prevalence of antibodies to *Toxoplasma gondii* in wild birds

Species	Country	No. examined	Positive (%)	Serologic test	Cut-off value	Reference
Struthioniformes (ostriches)						
Ostrich ( <i>Struthio camelus</i> )	Canada	973	2.9	MAT	1:25	Dubey et al. (2000b)
Ciconiiformes (egrets)						
Cattle egret ( <i>Bubulcus ibis</i> )	USA	40	2.5	IHAT	1:64	Burridge et al. (1979)
Anseriformes (ducks)						
Wood duck ( <i>Aix sponsa</i> )	USA	16	6	IHAT	1:64	Burridge et al. (1979)
Falconiformes (vultures)						
Vulture ( <i>Pseudogyps africanus</i> )	Nigeria	240	64.8	MAT	1:25	Arene (1999)
Turkey vulture ( <i>Cathartes aura</i> )	USA	2	50	IHAT	1:64	Franti et al. (1975)
Galliformes (turkeys)						
Turkey ( <i>Meleagris gallopavo</i> )	USA	130	10	MAT	1:25	Quist et al. (1995)
	USA	16	71	MAT	1:25	Lindsay et al. (1994)
Gruiformes (coots)						
American coot ( <i>Fulica americana</i> )	USA	38	3	IHAT	1:64	Franti et al. (1976)
Charadriiformes (gulls)						
Ring-billed gull ( <i>Larus delawarensis</i> )	USA	13	15.3	IHAT	1:64	Burridge et al. (1979)
Laughing gull ( <i>Larus atricill</i> )	USA	33	6	IHAT	1:64	Burridge et al. (1979)
Columbiformes (doves)						
Rock dove ( <i>Columba livia</i> )	Belgium	220	3.18	MAT	1:64	Cotteleer and Famerée (1978)
	Germany	49	2	DT	1:16	Niederehe (1964)
	Italy	108	3	DT	1:50	Mandelli and Persiani (1966)
	South Africa	16	100	IHAT	1:64	Mushi et al. (2001)
	USA	20	10	DT	1:16	Feldman and Sabin (1949)
	USA	15	6	DT	1:16	Gibson and Eyles (1957)
	USA	80	8.7	DT	1:16	Jacobs et al. (1952)
	USA	34	5.9	MAT	1:40	Kirkpatrick et al. (1990)
	USA	322	8.6	IHAT	1:16	Pendergraph (1972)

Spotted dove ( <i>Streptopelia chinensis</i> )	USA	134	8.2	DT	1:16	Wallace (1973)
Ruddy-ground dove ( <i>Columbina talpacoti</i> )	Panama	79	12.6	MAT	1:5	Frenkel et al. (1995)
Strigiformes (owls)						
Common barn-owl ( <i>Tyto alba</i> )	Germany	14	7.6	–	1:16	Niederehe (1964)
	USA	38	27.3	MAT	1:40	Kirkpatrick et al. (1990)
	USA	80	22.5	MAT	1:40	Kirkpatrick et al. (1990)
	USA	28	10.7	MAT	1:40	Kirkpatrick et al. (1990)
Passeriformes (various passerines)						
Plain wren ( <i>Thryothorus modestus</i> )	Panama	1	100	MAT	1:5	Frenkel et al. (1995)
Mockingbird ( <i>Mimus polyglottos</i> )	USA	133	0.75	IHAT	1:64	Burridge et al. (1979)
Robin ( <i>Turdus migratorius</i> )	USA	23	8.6	IHAT	1:64	Franti et al. (1975)
	USA	20	5	IHAT	1:64	Franti et al. (1976)
Clay-colored robin ( <i>Turdus grayi</i> )	Panama	12	16.6	MAT	1:5	Frenkel et al. (1995)
Crimson-backed tanager ( <i>Ramphocelus dimidiatus</i> )	Panama	8	12.5	MAT	1:5	Frenkel et al. (1995)
Blue-gray tanager ( <i>Thraupis episcopus</i> )	Panama	15	33	MAT	1:5	Frenkel et al. (1995)
Palm tanager ( <i>Thraupis palmarum</i> )	Panama	3	33	MAT	1:5	Frenkel et al. (1995)
Common grackle ( <i>Quiscalus quisqualis</i> )	USA	27	37	IHAT	1:64	Burridge et al. (1979)
Great-tailed grackle ( <i>Cassidix mexicanus</i> )	Panama	33	33	MAT	1:5	Frenkel et al. (1995)
Red-winged blackbird ( <i>Agelaius phoeniceus</i> )	USA	31	6.4	IHAT	1:64	Franti et al. (1975)
Brewer's blackbird ( <i>Euphagus cyanocephalus</i> )	USA	4	25	IHAT	1:64	Franti et al. (1975)
House sparrow ( <i>Passer domesticus</i> )	Czech Republic	227	12.3	IFAT	1:10	Literák et al. (1997)
Tree sparrow ( <i>Passer montanus</i> )	Czech Republic	41	4.9	IFAT	1:10	Literák et al. (1997)
Starling ( <i>Sturnus vulgaris</i> )	USA	563	4.8	IHAT	1:64	Haslett and Schneider (1978)
American crow ( <i>Corvus brachyrhynchos</i> )	USA	74	14	IHAT	1:64	Franti et al. (1976)

DT: dye test, IFAT: indirect fluorescent antibody test, IHAT: indirect hemagglutination test, LAT: latex agglutination test, MAT: modified agglutination test.

to have *T. gondii* antibodies. Reports of serologic prevalences in birds from the former USSR were tabulated by Jygiste and Gusev (1962), Pak (1976), and Beyer and Shevkunova (1986).

#### 4. Clinical toxoplasmosis in naturally infected birds

##### 4.1. *Columbiformes* (pigeons, doves)

There are several reports of clinical toxoplasmosis in the rock dove (common pigeon, *Columba livia*) (Carini, 1911; de Mello, 1915; Pires and Santos, 1934; Siim et al., 1963; Alosi and Iannuzzi, 1966), sometimes in epizootic form (Reis and Nóbrega, 1936; Springer, 1942; Johnson, 1943; Cassamagnaghi et al., 1952, 1977; Vogelsang and Gallo, 1954; Rodríguez, 1954; Wiktor, 1950; Paasch, 1983). Affected pigeons were anorexic, dull, emaciated, and had conjunctivitis with demonstrable organisms in ocular exudate and convulsions towards the time of death (Carini, 1911; Reis and Nóbrega, 1936). In pigeons that died, *T. gondii* was found in many tissues, especially in the lungs and spleen. In an outbreak reported by Johnson (1943) in US Army carrier pigeons in Panama, the birds became suddenly ill, had high fever, were weak, and several of them died. Birds that recovered had difficulty maintaining their balance. Mild encephalitis and neuritis were found in pigeons that recovered; Johnson (1943) isolated the parasite and maintained it in guinea pigs. It is uncertain whether there were other complicating factors for these epizootics. During recent years, such epizootics have not been reported.

Some species or breeds of pigeons appear to be more susceptible to clinical toxoplasmosis than others. For example, severe toxoplasmosis has occurred in crown pigeons, ornamental pigeons, and pigeons from Australia and New Zealand. Toxoplasmosis was diagnosed at necropsy in crown pigeons of the genus *Goura*: two from Belgium (Kageruka and Willaert, 1971; Tackaert-Henry and Kageruka, 1977), three *G. crista* from the Netherlands (Poelma and Zwart, 1972), one *G. victoria* from the US (Ratcliffe and Worth, 1951), two *G. victoria* from the Netherlands (Poelma and Zwart, 1972), four *G. victoria* from the Belgium (Tackaert-Henry and Kageruka, 1977), and four *G. scheepmaker* from the Netherlands (Poelma and Zwart, 1972); the diagnosis was confirmed by isolation of *T. gondii* from affected pigeons. Other reports of toxoplasmosis in ornamental pigeons were in one Pied Imperial pigeon from the Netherlands (Poelma and Zwart, 1972), in three Torres Strait pigeons (*Ducula spilorrhoa*), and one Wonga pigeon (*Leucosarcia melanoleuca*) from Australia (Hartley and Dubey, 1991); the diagnosis was confirmed by immunohistochemical staining with anti-*T. gondii* specific antibodies in pigeons from Australia (Hartley and Dubey, 1991). There is a report of toxoplasmosis in a bleeding heart dove (*Gallicolumba luzonica*) from the Netherlands (Poelma and Zwart, 1972).

Hubbard et al. (1986) reported an outbreak of toxoplasmosis in birds in a rain forest exhibit. Within 3 weeks, 13 of 20 birds died including seven Nicobar pigeons (*Caloenas nicobarica*), two luzon bleeding-heart pigeons (*Gallicolumba luzonica*) and one orange-breasted green pigeon (*Treron bicincta*). *T. gondii* was identified by immunohistochemical staining in 8 of the 13 dead birds. Included in the 13 dead birds were 2 crested wood partridges (*Rolulus rouloul*), and 1 yellow-headed rockfowl (*Picathartes gymnocephalus*). Because



eight birds with positive diagnosis were not identified in the paper by species, it is uncertain how many birds of each species had toxoplasmosis.

#### 4.2. *Passeriformes*

##### 4.2.1. *Canaries, finches*

Severe toxoplasmosis with an unusual clinical picture (blindness) has been reported in canaries (*Serinus canarius*) from Uruguay, Australia, Italy, New Zealand, UK, and the US. Because of the unusual nature of the disease this subject is discussed in detail.

Cassamagnaghi et al. (1952, 1977) isolated *T. gondii* from canaries that died in Uruguay. A total of 15 out of 18 birds from a breeder house died within 15 days. Affected birds had splenomegaly, necrotic lesions in the lungs and spleen, enteritis, and hepatic degeneration.

Parenti et al. (1986) and Cerruti Sola et al. (1985) (both reports refer to the same material) reported toxoplasmosis in an Italian aviary housing small passerine birds. Out of a total of 230 birds, approximately 115 canaries (*S. canaria*), and 46 greenfinches (*Carduelis chloris*) had been born in captivity and the remaining birds, 27 goldfinches (*C. carduelis*), 20 siskins (*C. spinus*), 11 bullfinches (*Pyrrhula pyrrhula*), and 9 Linnets (*C. cannabina*) were captured in the wild. Within 2 weeks of the start of the outbreak, 90% of the birds born in captivity died; overall 26% of the bird population died. Clinical signs included weight loss, diarrhea, and dyspnea. A total of 22 out of 25 birds had antibodies to *T. gondii* ( $\geq 1:64$ ) in the latex agglutination test (LAT). Four months after the onset of the outbreak some birds had conjunctivitis, blepharitis and unilateral atrophy of the eye. *T. gondii* was isolated in mice inoculated with eye suspensions of animals with ocular atrophy. Histopathologically, the most severe lesions were in the lungs. *T. gondii* was identified in sections of several tissues. Unfortunately the number and species of birds examined histopathologically and the number of birds whose tissues were bioassayed in mice were not given.

Vickers et al. (1992) reported blindness associated with *T. gondii* in canaries from aviaries in New Zealand and Australia (Sydney and Tasmania). The birds had crusty exudates around the eye lids, and some eyeballs had collapsed. The birds appeared otherwise alert and were eating. Half of the affected birds had evidence of encephalitis (head twitch, walking in circles). A total of 12 canaries were examined at necropsy. Of the 24 eyes examined histologically, 18 had lesions including acute, severe, diffuse nonsuppurative inflammation of choroid with or without retinal involvement (Figs. 2 and 3). There was osseous replacement of the globe and atrophy of the periocular tissue resulting in a sunken appearance of the eye. Numerous *T. gondii* tachyzoites were seen in the choroid, retina, vitreous, and even in the lens (Fig. 3). One bird had cataracts. Diagnosis was confirmed by immunohistochemical demonstration of *T. gondii* in ocular lesions and by isolation of *T. gondii* from affected eyes by bioassay in mice. In addition to direct involvement of *T. gondii* in inner layers of the eye, there was nonsuppurative inflammation of the optic nerve with loss of myelinated axons, and there was histologic evidence of encephalitis. This is the most convincing evidence of *T. gondii*-associated chororetinitis in any host.

Similar episodes of blindness and encephalitis were reported from another region of Australia. Several birds in a flock of 40 canaries in Victoria, Australia, developed blindness and neurologic signs (Lindsay et al., 1995). Of the eight birds that died or were euthanized, two were studied histologically. Both birds had bilateral ophthalmitis, but *T. gondii* was

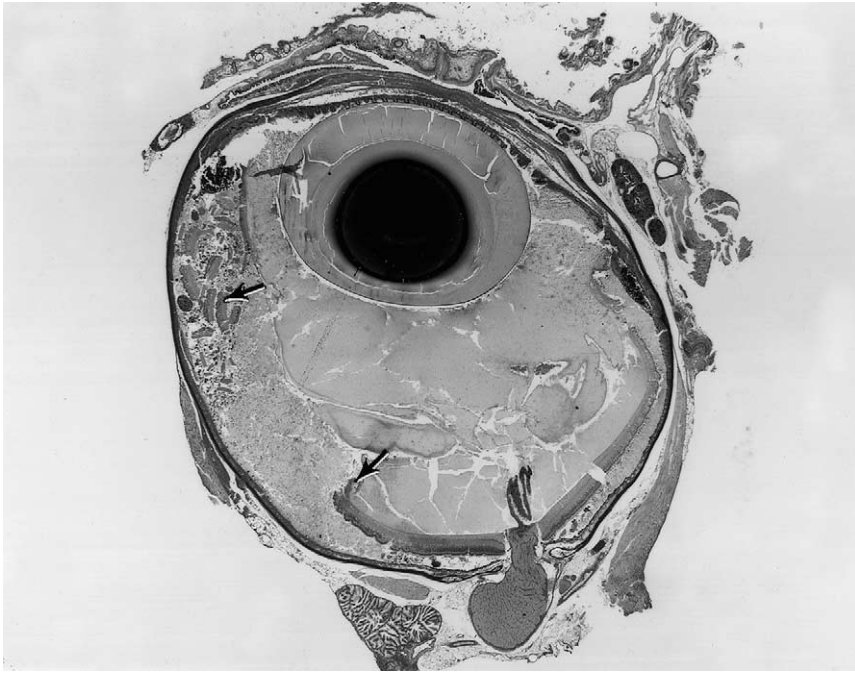


Fig. 2. Section of an eye of a canary naturally-infected with *T. gondii*. This section is through the optic nerve and the lens. The choroid and retina are degenerating and fragments (arrows) are floating in the vitreous (H and E).

not found in their eyes. Only tissue cysts were seen in the canary brain and they were not associated with inflammation, indicating the birds were developing immunity to *T. gondii*. Treatment with trimethoprim (80 mg/ml) and sulfadiazine (400 mg/ml) in drinking water for 14 days was apparently successful as no new cases were seen.

Gibbens et al. (1997) reported of an outbreak in a group of 47 breeding canaries in an aviary from the UK. The most prominent feature of this outbreak was blindness in the absence of other clinical signs. The eyes became dull, sightless, closed up and sunken in the head (Gibbens et al., 1997). Of the 44 birds observed, 16 had eye lesions, 5 of them were blind, but only 1 bird died. Nine clinically affected canaries were examined at necropsy, all of them had eye lesions and three of them had pneumonia. Two birds were studied histologically, both had nonsuppurative encephalitis associated with *T. gondii* tissue cysts but no lesions in the eye. Antibodies to *T. gondii* (titers 1:64, 1:256) were found in sera of two of the four birds examined by the LAT.

Williams et al. (2001) reported blindness in 9 of 15 common yellow canaries in an indoor aviary in Michigan, USA. Blindness was noticed intermittently over a period of 3 months, two birds had torticollis. It was remarkable that the affected canaries could eat, court and lay eggs. One sick canary (bird A) with torticollis was able to perch, but stumbled when moved to a flat surface; this bird was euthanized. Necropsy examination was performed on two birds, including bird A and a dead bird (bird B). Bird B was autolyzed, but had histologic evidence of *T. gondii*-associated encephalitis. Lesions were confined to the brain and the

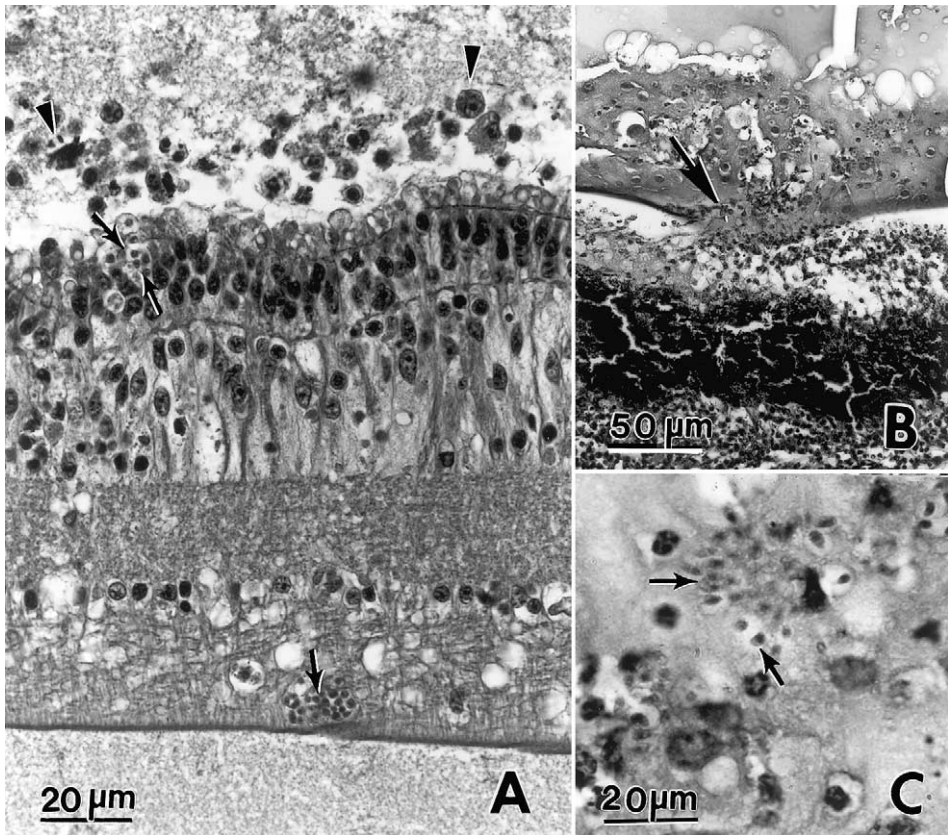


Fig. 3. Sections through eyes of canaries naturally-infected with *T. gondii*: (A) retina with tachyzoites (arrows) in retinal layers and desquamation of tachyzoites and retinal cells in the vitreous (arrowheads); (B) lens with focal inflammation and tachyzoites (arrow); the choroid is at the bottom of the picture; (C) higher magnification of lesion in the lens to show tachyzoites (arrows) (H and E).

eyes of bird A. *T. gondii* was found in the encephalitic lesions. The eye lesions consisted of anterior and posterior uveitis and swelling of the lenticular fibers in the lens. There was severe choroiditis, focal necrosis and detachment of the retina; tachyzoites were seen in the nerve fiber layer of the retina. *T. gondii* tissue cysts were identified by electron microscopy and indirect fluorescent antibody test in the brain of the canaries.

In conclusion, toxoplasmosis should be considered in the differential diagnosis of blindness in canaries and serologic tests other than LAT, and indirect hemagglutination test (IHAT) should be used to evaluate antibodies to *T. gondii* in clinically affected birds (Vickers et al., 1992; Gibbens et al., 1997).

#### 4.2.2. Mynahs

Dhillon et al. (1982) reported toxoplasmosis-like illness in 23 mynahs (*Acridotheres* spp.) imported from Mexico. Lesions and parasites were seen in the liver, lungs, and spleen.

Macrophages in the liver contained 1–3  $\mu\text{m}$  sized protozoans. In my view, this outbreak was misdiagnosed as toxoplasmosis. Rather, the parasite and the lesions are identical to those of *Atoxoplasma* (Partington et al., 1989). The parasites illustrated are half the size of *T. gondii* (see Section 6).

Also, toxoplasmosis was histologically diagnosed in a gold crested mynah (*Ampeliceps coronatus*) in captivity in the Netherlands.

#### 4.2.3. Sparrows

Although sparrows in nature can harbor live *T. gondii* (Table 1), there is no confirmed report of clinical toxoplasmosis in naturally-infected sparrows.

#### 4.2.4. Crows

Fatal toxoplasmosis has been reported once in crows (Work et al., 2000). The Hawaiian crow (*Corvus hawaiiensis*) is an endangered species with <25 birds left in captivity or in the wild (Work et al., 2000). Toxoplasmosis was diagnosed in five 321–791-day-old birds that were captured or found dead in the wild; all were wearing radiocollars. Two birds were found dead and partially scavenged. The main lesion in birds nos. 1 and 2 was encephalitis associated with tissue cysts (Fig. 4B). Bird no. 3 was completely eaten by maggots except its head; the carcass was foul smelling and not studied histologically; *T. gondii* was isolated from brain of bird no. 3 by bioassay. Bird no. 4 had generalized acute toxoplasmosis involving the spleen, liver, brain, adrenal gland, and skeletal muscle. Numerous tachyzoites were present in liver and spleen and *T. gondii* was isolated by bioassay from the brain of this crow. Bird no. 5 had serologic evidence of *T. gondii* infection with antibody titer of 1:1600 in the modified agglutination test (MAT). The bird was found to be depressed and losing weight. After administration of an anticoccidial diclazuril (10 mg/kg) for 18 days its physical condition improved and the bird was released in the wild.

#### 4.2.5. Other passerines

Toxoplasmosis was immunohistologically diagnosed in a satin bowerbird (*Ptilonorhynchus violaceus*), in one regent bowerbird (*Sericulus chrysocephalus*) and in a red-whiskered bulbul (*Pycnonotus jocosus*) in Australia (Hartley and Dubey, 1991); the diagnosis was confirmed immunohistochemically. Vogelsang and Gallo (1954) found *T. gondii* in the spleen and livers of *Holoquiscalus lugubris*.

### 4.3. Psittaciformes

#### 4.3.1. Budgerigars

Toxoplasmosis was suspected in two budgerigars (*Melopsittacus undulatus*) in Switzerland (Galli-Valerio, 1939). Other than enlargement of the spleen, no other lesions were seen. The birds were suspected to have psittacosis and, therefore, liver homogenate was inoculated into mice. *T. gondii* tachyzoites were seen in impression smears of tissues of mice that died following inoculation with avian tissues. Thus, evidence for toxoplasmosis was based on bioassay.

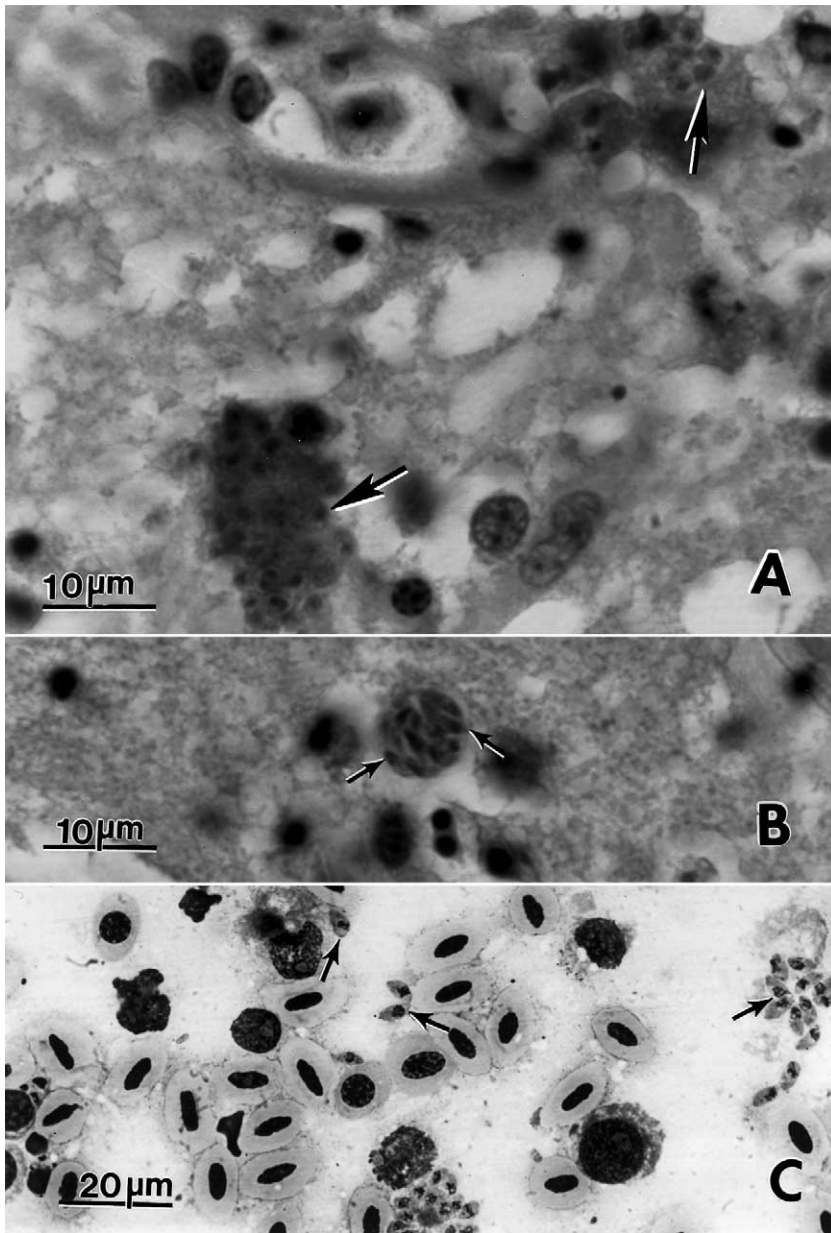


Fig. 4. Toxoplasmosis in Hawaiian crows (*Corvus hawaiiensis*): (A) cerebrum with tachyzoites (arrows) in an area of necrosis (H and E); (B) cerebrum with a small tissue cyst with thin cyst wall and bradyzoites with terminal nuclei (H and E); (C) impression smear of spleen with numerous tachyzoites (arrows). (Giemsa).

#### 4.3.2. Parrots

Toxoplasmosis was diagnosed in one Regent parrot (*Polytelis anthopeplus*), and in one superb parrot (*P. swansonii*) that had died in a zoo in Australia; the diagnosis was confirmed immunohistologically (Hartley and Dubey, 1991).

#### 4.3.3. Lories

There is one report of toxoplasmosis in a red lory (*Eos bornea*) from the US (Howerth et al., 1991). The lory had been hatched in an outdoor aviary, reared by the parents for 2 weeks, and then reared by hand for 1 week. It died at 3 weeks of age, probably due to respiratory distress. Grossly, the lungs were consolidated and sank in formalin. Microscopic lesions were necrotizing myocarditis, hepatitis and intestinal pneumonia. Tachyzoites were seen in lesions and the diagnosis was confirmed by immunohistochemical staining with anti-*T. gondii* antibodies and by electron microscopy of tissue cysts.

#### 4.3.4. Other psittacines

Toxoplasmosis was diagnosed in a Swainson's lorikeet (*Trichoglossus moluccanus*) from the Netherlands (Poelma and Zwart, 1972) and in one crimson rosella (*Platycercus elegans*) from Australia (Hartley and Dubey, 1991).

### 4.4. Strigiformes (owls)

Clinical toxoplasmosis was reported in a barred owl (*Strix varia*) from Canada that died 16 days following a collision with a car (Mikaelian et al., 1997). Numerous 1 mm diameter pale areas were scattered throughout the liver. Histologically, the liver lesions consisted of multifocal necrotic areas surrounded by inflammatory cells (Fig. 5). Numerous tachyzoites were seen in lesions and the diagnosis was confirmed immunohistochemically (Fig. 5). Few tachyzoites were seen in the duodenum; the brain was not examined. Whether stress led to relapse of latent infections or the owl ingested *T. gondii*-infected food while hospitalized could not be determined.

### 4.5. Galliformes (turkeys, partridges, capercaillies, francolin)

#### 4.5.1. Turkeys

Clinical toxoplasmosis is considered rare in wild turkeys (*Meleagris gallapavo*). Only two cases have been reported in wild turkeys, both from Georgia, USA (Howerth and Rodenroth, 1985; Quist et al., 1995). Both turkeys were found dead in the field and both had multiple small necrotic foci in the spleen and liver. Protozoans resembling *T. gondii* were found in sections of spleen, lung, adrenal, brain, kidney, liver, proventriculus, esophagus and colon of the first turkey, this turkey probably died because of toxoplasmic pneumonia (Howerth and Rodenroth, 1985). In the second turkey, *T. gondii*-like organisms were found in sections of spleen, liver, and kidneys, and the diagnosis was confirmed immunohistochemically (Quist et al., 1995).

There is one report of toxoplasmosis in domestic turkeys in a flock in Germany (Schulte, 1954). A total of 4 out of 10 birds died. They were emaciated and had encephalitis.

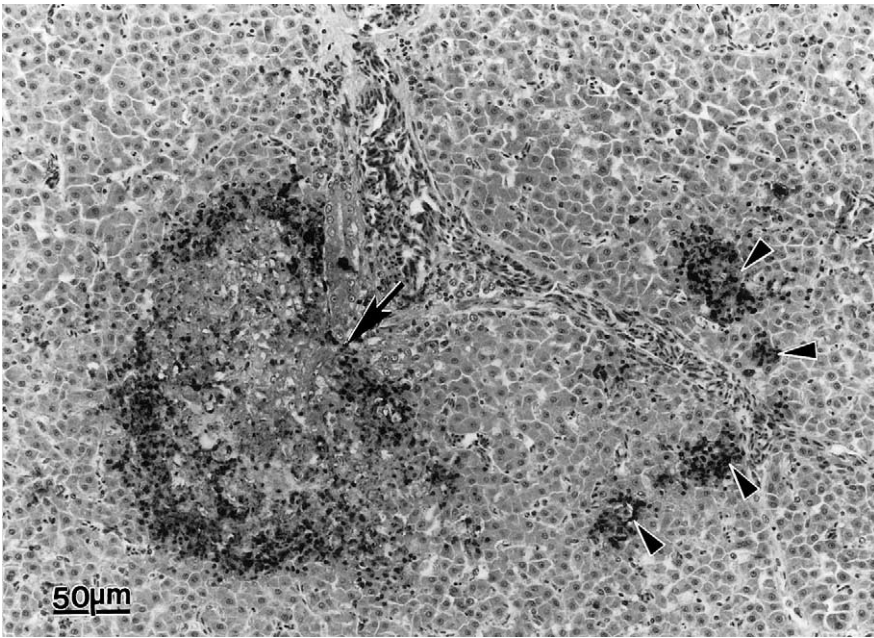


Fig. 5. Multiple foci (arrow and arrowheads) of necrosis in periportal area of the liver of a naturally-infected owl (*Strix varia*) from Canada. Numerous *T. gondii* tachyzoites (all black areas) are present in areas of necrosis. Immunohistochemical stain with anti-*T. gondii* antibodies.

#### 4.5.2. Partridges

There is only one report of clinical toxoplasmosis in partridges (*Perdix perdix*) by Pokorný (1955). Partridges caught in the wild in the Czech Republic died in captivity soon after they were trapped; *T. gondii* were found in smears of liver and spleen of three of 24 partridges that died.

#### 4.5.3. Capercaillies

A toxoplasmosis-like illness has been recognized for many years as the cause of mortality in capercaillie (*Tetrao urogallus*), a game galliform bird in Europe (Hülphers et al., 1947; Gustafsson et al., 1997). Parasites and lesions are confined to the CNS. Recent studies indicate that the parasite is a species of *Sarcocystis* and not *T. gondii* (Gustafsson et al., 1997; Dubey et al., 1998) (see Section 6). This parasite has not yet been cultivated in vitro.

#### 4.5.4. Francolin

Work et al. (2002) reported toxoplasmosis in a free-ranging Erckel's francolin (*Francolinus erckelii*) found dead on Kauai island, Hawaii, USA. Gross lesions included focal discoloration of the liver and the heart, and edematous lungs. Microscopically, there was severe myocardial necrosis, hepatic necrosis, nonsuppurative encephalitis, and splenic necrosis. Numerous tachyzoites were found in lesions and the diagnosis was confirmed immunohistologically.

#### 4.6. *Anseriformes* (geese, ducks)

Toxoplasmosis was diagnosed in two magpie geese (*Anseranas semipalmata*) raised in captivity in a zoo (Dubey et al., 2001a). Both geese died suddenly without apparent clinical signs. Lesions and *T. gondii* were found in many organs including the bursa of Fabricius. Toxoplasmic pneumonia and hepatitis were considered to be the main cause of death. Numerous tissue cysts were seen in the liver of both geese. The diagnosis was confirmed by immunohistochemical staining. Antibodies (MAT titers 1:25 and 1:100) were found in two of 11 sera from other geese tested (Dubey et al., 2001a).

Work et al. (2002) reported acute toxoplasmosis in two (one male, one female) endangered Hawaiian goose nene goslings (*Nesochen sandicensis*) at a zoo in Maui, Hawaii, USA. Both birds died suddenly and had edematous and consolidated lungs. Histologically, the female gosling had severe interstitial mononuclear cell pneumonia, necrosis in liver, brain, heart and muscles. There was also full thickness necrosis of intestinal wall extending through lamina propria and the muscular layers. Tachyzoites were found in lesions and the diagnosis was confirmed immunohistochemically. The intestinal and hepatic lesions were suggestive of recently acquired toxoplasmosis, probably by ingesting food contaminated with oocysts.

There is no report of clinical toxoplasmosis in wild ducks and there is only one report of clinical toxoplasmosis in domestic ducks (Boehringer et al., 1962) from Argentina.

#### 4.7. *Struthioniformes*, *Rheiformes*, *Casuariformes*

Although there is no proven clinical case of toxoplasmosis in ostriches, Orosz et al. (1992) reported MAT titers (1:4096) in rhea (*Rhea americana*) and in cassowary (*Casuarius casuarius*) suspected to have clinical toxoplasmosis.

#### 4.8. *Sphenisciformes* (penguins)

There are a few cases of toxoplasmosis that were diagnosed histologically in penguins. In the USA, Ratcliffe and Worth (1951) diagnosed toxoplasmosis in four captive Humboldt penguins (*Spheniscus humboldti*), two magellanic penguins (*S. magellanicus*), and one black-footed penguin (*S. demersus*) that had died in a zoo. In Australia, Mason et al. (1991) reported severe toxoplasmosis in a Little penguin (*Eudyptula minor*) and the diagnosis was confirmed immunohistochemically. Toxoplasmosis was diagnosed in an Indian Pangolin (*Manis crassi caudato*) from the Netherlands (Kageruka and Willaert, 1971).

#### 4.9. *Pelecaniformes* (Sulidae)

Work et al. (2002) found toxoplasmosis in a red-footed booby (*Sula sula*) adult found weak on the Oahu island, Hawaii, USA. The bird was admitted for rehabilitation at a local zoological park and died 40 days later. The main gross lesions included heavy wet lungs that sank in formalin, friable spleen, and engorged cerebral vasculature. Histologic examination revealed marked diffuse necrosis and mononuclear cell infiltration in the lungs associated with tachyzoites, suppurative periportal cell infiltration of the liver, severe mononuclear



inflammation associated with tachyzoites in the heart, focal neuronal necrosis of the cerebrum associated with tissue cysts, and focal necrosis and non-suppurative inflammation in the adrenal gland. Tachyzoites were found in lesions and the diagnosis was confirmed immunohistochemically.

## 5. Experimental infections

### 5.1. *Galliformes* (comparative susceptibility of gallinaceous birds to *T. gondii*)

Turkeys (*Meleagris gallopavo*), bobwhites (*Colinus virginianus*), Japanese quails (*Coturnix japonica*), pheasants (*Phasianus colchicus*), rock partridges (*Alectoris graeca*), partridges (*Perdix perdix*), and helmeted guineafowl (*Numida meleagris*) were fed graded doses of *T. gondii* oocysts (Table 3). Birds were bled before and after feeding oocysts, sera were examined for *T. gondii* antibodies by the LAT, MAT, DT, and ELISA in case of turkeys (Dubey et al., 1993a,b, 1994a,b, 1995) and by the indirect fluorescent antibody test (IFAT) in turkeys, rock partridges, and helmeted guineafowl (Sedlák et al., 2000).

Antibodies to *T. gondii* were not detectable by the DT in any of these species of birds tested, and the IHAT and LAT were found inferior to MAT. Using the MAT, *T. gondii* antibodies were detected sooner and in higher titers than with the IHAT and LAT. Antibodies were successfully detected in chicken and turkey sera using the ELISA; this test was not tried in the other avian species. The IFAT was also found useful to detect *T. gondii* antibodies in gallinaceous birds.

Of the avian species listed in Table 3, the rock partridge (*A. graeca*) was the most susceptible to oral infection with oocysts. Rock partridges fed  $10^5$  *T. gondii* oocysts died, whereas pheasants fed  $10^5$  oocysts of the same isolate survived. Birds that died acutely, succumbed from enteritis. Grossly, the intestines were hyperemic and had fibrino-necrotic enteritis, sometimes with desquamation of the entire mucosa. Microscopically, the enteric lesions resulted from the multiplication of *T. gondii* tachyzoites in the lamina propria. The parasites multiplied in virtually all cells of the lamina propria including endothelial cells (Fig. 6). Subsequently, there was oozing out of the contents of the lamina propria into the intestinal lumen. Desquamation of surface epithelium led to ulceration; sometimes ulcers extended to the serosal layer (Fig. 7). Birds that recovered from enteritis usually became clinically normal. Encephalitis was found in few birds that survived 15 days postinoculation (p.i.) (Dubey et al., 1994a,b). Swarms of *T. gondii* tachyzoites invaded neuropil (Fig. 8A). Tissue cysts (Fig. 8B) were seen in birds that survived 3 weeks p.i. Lesions were not seen in the eyes of any of the birds fed oocysts.

The two species of chuckars (*A. graeca* and *Alces chuckars*) were remarkably different in their susceptibility to *T. gondii*. As mentioned earlier, *A. graeca* was one of the most susceptible avian species to *T. gondii*; two of six birds fed 10 oocysts died of acute toxoplasmosis (Table 3). Although results are not exactly comparable because different strains of *T. gondii* were used, *A. chuckar* fed as many as  $10^5$  oocysts remained healthy (Table 3). The partridges (*P. perdix*) on the other hand were quite susceptible to *T. gondii* infection (Table 3). The pheasants (*P. colchicus*) and the guineafowl (*N. meleagris*) were less susceptible to clinical toxoplasmosis than chuckars or partridges (Table 3).

Table 3

Experimental toxoplasmosis in gallinaceous birds (except chickens) fed *Toxoplasma gondii* oocysts

Species	No. of oocysts fed	<i>T. gondii</i> strain	No. died/ no. fed	Clinical disease	Day of death	Reference
Japanese quail ( <i>Coturnix japonica</i> )	10 <sup>5</sup>	GT-1	6/6	Acute	6–8	Dubey et al. (1994a)
	10 <sup>3</sup>	GT-1	5/6	Acute	8–23	
	10 <sup>5</sup>	Me-49	1/6	Mild disease	9	
	10 <sup>3</sup>	Me-49	1/6	Mild disease	16	
Bobwhites ( <i>Colinus virginianus</i> )	10 <sup>5</sup>	GT-1	2/6	Acute, chronic	6, 7	Dubey et al. (1993b)
	10 <sup>4</sup>	GT-1	1/6	Acute, chronic	8	
	10 <sup>5</sup>	Me-49	1/6	Acute, chronic	18	
	10 <sup>4</sup>	Me-49	0/6	None		
Pheasants ( <i>Phasianus colchicus</i> )	10 <sup>4</sup>	GT-1	1/5	Depressed	19	Dubey et al. (1994b)
	10 <sup>5</sup>	Me-49	0/6	None		
	10 <sup>4</sup>	Me-49	0/6	None		
Turkeys ( <i>Meleagris gallopavo</i> )	10 <sup>5</sup>	Me-49	3 <sup>a</sup> /8		12–14	Dubey et al. (1993a)
	10 <sup>4</sup>	Me-49	0/6	None		
	10 <sup>5</sup>	K-7	0/5	None		Sedlák et al. (2000)
Rock partridges ( <i>Alectoris graeca</i> )	10 <sup>4</sup>	GT-1	6/6	Acute	4–6	Dubey et al. (1995)
	10 <sup>4</sup>	Me-49	5/6	Acute	7–11	
	10 <sup>3</sup>	Me-49	4/6	Acute	10, 11	
	10 <sup>2</sup>	Me-49	4/6	Acute	10–14	
	10	Me-49	2/6	Acute	12, 13	
Chukars ( <i>Alectoris chukar</i> )	10 <sup>5</sup>	K-7	0/5	None		Sedlák et al. (2000)
	10 <sup>3</sup>	K-7	0/5	None		
Partridges ( <i>Perdix perdix</i> )	10 <sup>5</sup>	K-7	6/8	Acute	6–10	
	10 <sup>3</sup>	K-7	2/5	Acute, chronic	16, 16	
Helmeted guineafowl ( <i>Numida meleagris</i> )	10 <sup>5</sup>	K-7	0/5	None		
	10 <sup>3</sup>	K-7	0/5	None		

<sup>a</sup> Died of concurrent aspergillosis.

Results of experimental infections demonstrate that domestic turkeys are resistant to clinical toxoplasmosis (Drobeck et al., 1953; Simitch et al., 1961). Even 1 or 2-week-old turkeys inoculated intraperitoneally with millions of RH strains tachyzoites became infected but did not develop clinical signs; all 22 turkeys so infected harbored *T. gondii* in their tissues (Drobeck et al., 1953). Similar results were obtained by feeding *T. gondii* oocysts (Dubey et al., 1993a; Sedlák et al., 2000). Fourteen turkeys were fed 10<sup>4</sup> or 10<sup>5</sup> oocysts (Table 3). Three turkeys died or were euthanized 12 or 14 days p.i., but the deaths were considered due to an infection with *Asperigillus*-like fungus (Dubey et al., 1993a). Viable *T. gondii* was recovered from tissues of all turkeys by bioassay in mice and all turkeys developed antibodies to *T. gondii* detectable by MAT, ELISA, LAT or IHAT but not by the DT (Dubey et al., 1993a). The ELISA did not work well when diluting the turkey serum in 0.85% NaCl solution, but worked well with 7.0% NaCl solution. In the study reported by Sedlák et al. (2000) all five turkeys fed 10<sup>5</sup> oocysts became infected, but did not develop clinical signs.

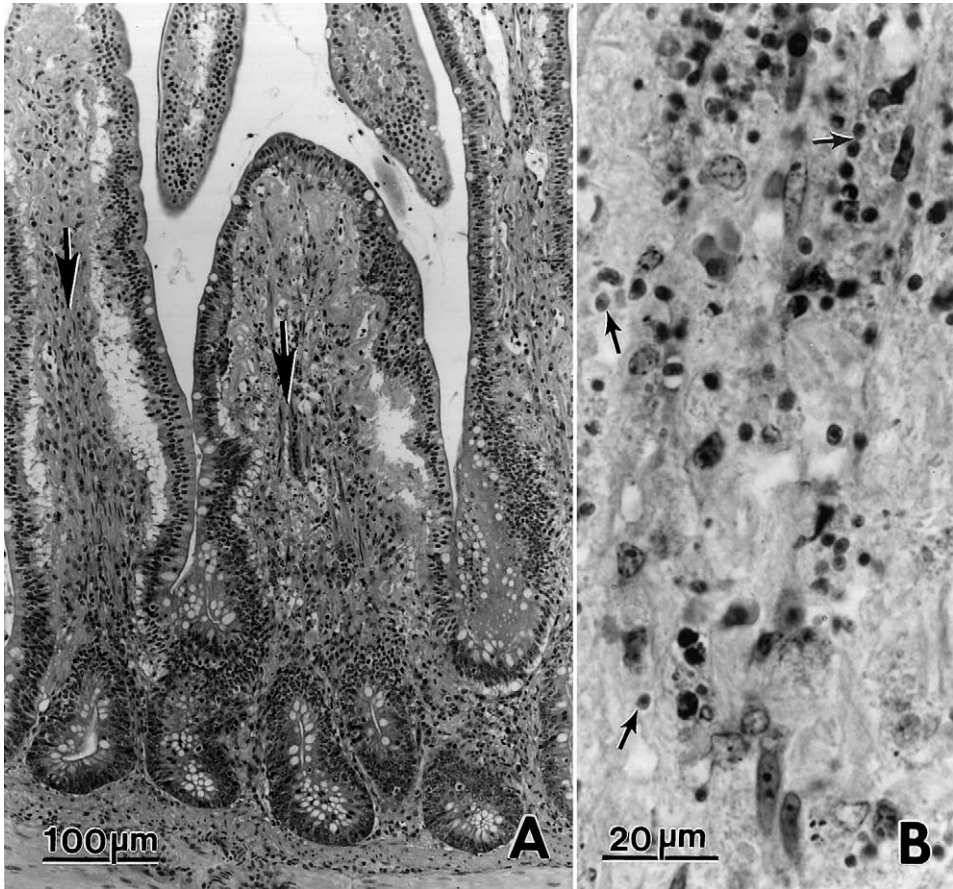


Fig. 6. Lesions and tachyzoites in sections of small intestines of rock partridges fed *T. gondii* oocysts (H and E): (A) tachyzoites, edema and necrosis in the lamina propria (arrows), the surface epithelium is not parasitized, day 5 p.i.; (B) lamina propria with numerous tachyzoites (arrows) destroying host cells, day 7 p.i.

Simitch et al. (1959, 1961, 1963, 1965) attempted to orally infect ducks, pigeons, geese, quails, and guinea-fowls with tachyzoites and tissue cysts of *T. gondii*.

### 5.2. *Columbiformes* (pigeons, doves)

Carini and Maciel (1913) and Nicolau and Kopciowska (1935) infected pigeons with homogenates of tissues of dogs that had died of toxoplasmosis and concluded that the disease in dogs was the same as in pigeons. Reis and Nóbrega (1936) induced fatal toxoplasmosis in pigeons by intramuscular inoculation of organ suspension of pigeons affected with toxoplasmosis. All pigeons became ill and died within 10 days. Nóbrega and Reis (1942) maintained *T. gondii* by passage in pigeons for 20 passages and the strain was infective to mice, guinea pigs, rabbits, and chickens.

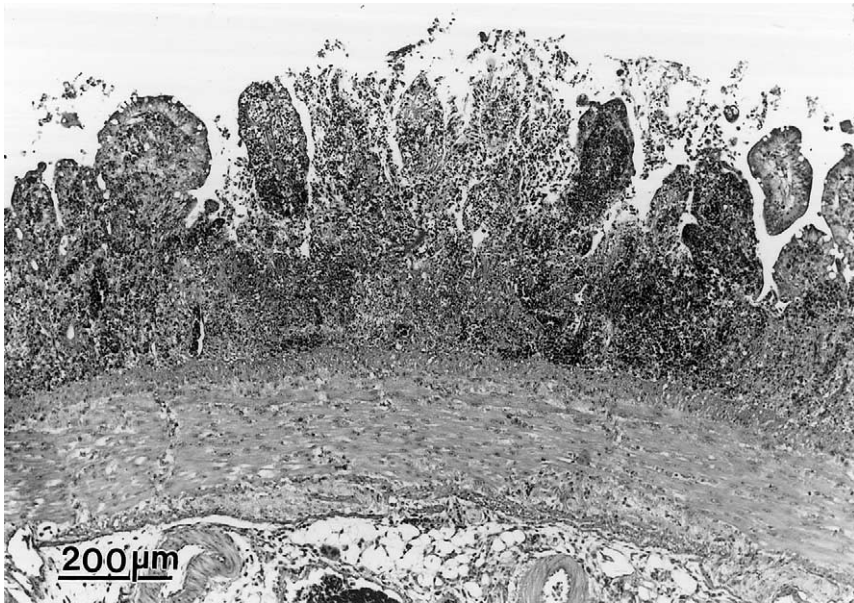


Fig. 7. Transmur al necrosis, infiltration of mixed leukocytes, and almost total desquamation of surface epithelium of the small intestine in a rock partridge fed *T. gondii* oocysts, day 5 p.i. (H and E).

During the 1940s and 1950s, pigeons were inoculated with *T. gondii* tachyzoites by various parenteral routes to study parasitemia and the persistence of *T. gondii*. Pigeons inoculated with tachyzoites of the mouse virulent strains (such as the RH strain) developed parasitemia and about half of them died with acute toxoplasmosis involving many organs (Pixell, 1913; Carini, 1911; Laveran and Marullaz, 1913; Nóbrega and Reis, 1942; Manwell and Drobeck, 1951; Drobeck et al., 1953; Frenkel, 1953; Jacobs et al., 1953; Pak, 1971). There was a high level of parasitemia even in birds that survived (Jacobs et al., 1953). Severe necrotic lesions were seen in many tissues of the pigeons that died acutely, including their eyes and nasal passages (Frenkel, 1953). Pigeons developed high levels of antibodies in the DT, but some became seronegative with no detectable antibodies in the undiluted serum; these pigeons had detectable parasites in their tissues by bioassays in pigeons (Drobeck et al., 1953; Jacobs et al., 1953). *T. gondii* was recovered from tissues of pigeons as long as 33 months after infection (Jacobs et al., 1953). Not all strains of *T. gondii* were virulent to pigeons (Frenkel, 1953; Jacobs et al., 1953).

Pigeons were reported to be highly susceptible to oral infection with *T. gondii* oocysts (Biancificiori et al., 1986). Four groups of five pigeons were fed 50, 500, 1000 or 5000 *T. gondii* oocysts. All pigeons died of acute toxoplasmosis, 13–20 days after feeding 500 or more oocysts. Pigeons fed 50 oocysts became infected, but did not become ill. Pigeons fed oocysts developed antibodies to *T. gondii* detectable by ELISA (Biancificiori et al., 1986).

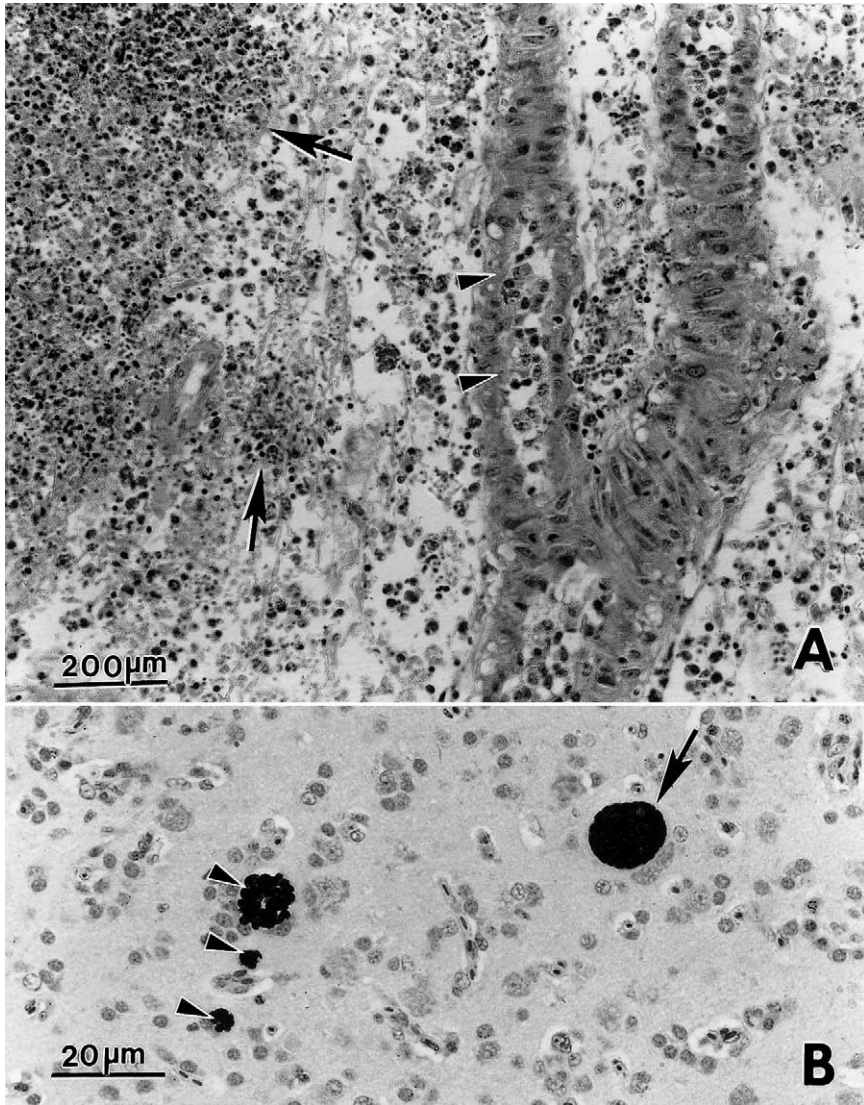


Fig. 8. Lesions and parasites in sections of the brains of birds fed *T. gondii* oocysts: (A) cerebrum of a Japanese quail with suppurative meningoencephalitis. Note extensive necrosis, microabscess (arrows), and periarteritis (arrowheads), day 16 p.i. (H and E); (B) cerebrum of a pheasant. Individual and groups of *T. gondii* without any host reaction in the brain of a partridge fed oocysts. Immunohistochemical stain with anti-*T. gondii* antibodies. The large group of *T. gondii* (arrow) is probably a tissue cyst, day 19 p.i.

Wallace (1973) fed an unknown number of *T. gondii* oocysts to nine pigeons (*C. livia*), 31 barred doves (*Geopelia striata*), and 12 spotted doves (*Streptopelia chinensis*). All 31 barred doves died between 6 and 11 days whereas other birds survived at 22 days; *T. gondii* was isolated from three of three pigeons, two of three doves,

and one of one spotted dove. Thus, barred doves were the most susceptible to *T. gondii* oocysts.

### 5.3. *Passeriformes* (canaries, sparrows, grackles, budgerigars)

Canaries inoculated parenterally with mammalian *T. gondii* died within 12 days (Wolfson, 1941; Cassamagnaghi et al., 1952, 1977). Parasites were found in most visceral tissues, especially in liver and spleen. Birds died between 7 and 13 days after inoculation with *T. gondii*, irrespective of the dose (Cassamagnaghi et al., 1952, 1977). Similar results were reported by Lainson (1955) who inoculated three canaries intraperitoneally with an isolate of *T. gondii* from a rabbit. One canary died on day 9, one on day 14 and the third was euthanized on day 14. Tachyzoites were found in tissues of all three birds. In addition, tissue cysts were seen in the brain of the canaries examined day 14 p.i.

Experimentally, sparrows are relatively resistant to *T. gondii*, but results may vary depending on the strain, stage and number of *T. gondii* inoculated (Wallace, 1973; Literák et al., 1999). Most sparrows inoculated parenterally with numerous tachyzoites of the mouse virulent strains (such as the RH strain) died of acute infection (Nicolau and Kopciowska, 1935; Manwell et al., 1945; Manwell and Drobeck, 1951; Drobeck et al., 1953) and sparrows fed a relatively high dose of  $10^5$  oocysts also died of acute toxoplasmosis (Pak, 1974). Recently, Literák et al. (1999) fed graded doses of  $1$ – $10^4$  oocysts to sparrows; all birds remained clinically normal. Sparrows fed one oocyst each developed low titers (IFAT 1:20 or less), but the parasite was not recovered from their tissues. *Toxoplasma gondii* was isolated from one of six sparrows fed ten oocysts, three of six fed 100 oocysts, four of six fed 1000 oocysts, and five of six fed 10,000 oocysts. The IFAT were generally  $>1:80$  in sparrows that were proven to be infected with *T. gondii*.

In one study, at least 8 of 31 song sparrows (*Melospiza melodia*) and four of seven purple grackles (*Quiscalus quiscula*) inoculated intraperitoneally or intracerebrally with millions of RH strain tachyzoites became infected with *T. gondii* (Manwell and Drobeck, 1951).

Dubey and Hamir (2002) studied the susceptibility of budgerigars (*M. undulatus*) to graded doses of *T. gondii* oocysts. Sixteen budgerigars were divided into four groups (A–D) of four. Birds in groups A–C were fed 100,000, 1000 or 100 infective oocysts of the VEG strain of *T. gondii*, respectively. Budgerigars in group D were not fed oocysts and served as controls. All four birds in group A died (or were killed) because of acute severe enteritis 5 or 6 days after feeding oocysts (DAFO). Three of the four birds in group B were killed (or died) because of toxoplasmosis 9 or 14 DAFO. One budgerigar in group C and the four budgerigars in group D remained healthy and were killed 35 or 39 DAFO. *T. gondii* was demonstrated in tissues of all budgerigars fed oocysts. The control budgerigars remained clinically normal and had no evidence of *T. gondii* exposure. These results indicate that, compared to other passerines, budgerigars are relatively resistant to clinical toxoplasmosis.

### 5.4. *Strigiformes*, *Falconiformes* (owls, hawks, kestrels)

Experimental data indicate that owls and other predatory birds are resistant to *T. gondii*. Seven owls (one great horned owl, *Bubo virginianus*, three barred owls, *S. varia*, and three screech owls, *Asio otus*) and three red-tailed hawks (*Buteo jamaicensis*) fed *T. gondii* tissue

cysts became infected, but did not develop clinical signs (Lindsay et al., 1991; Dubey et al., 1992). *T. gondii* was isolated from all ten birds and all birds developed antibodies to *T. gondii*. The MAT titers of 1:80 or more were found in all birds. In another study, three great horned owls and one American kestrel (*Falco sparverus*) fed *T. gondii* did not develop clinical signs (Miller et al., 1972).

## 6. Diagnosis

Serologic, histopathologic, immunohistochemical, and molecular examinations can aid diagnosis and this subject has been discussed in detail elsewhere (Dubey and Beattie, 1988; Dubey et al., 1993a,b; Dubey and Odening, 2001). Among different serologic tests available, the MAT is most useful because it is sensitive, specific, does not require special equipment, and works well with all species of birds tested (see Section 5). *T. gondii* DNA can be detected by using *T. gondii*-specific primers with PCR. However, in most cases, the diagnosis will be made by histologic examination of birds submitted for necropsy examination and in most cases the tissues have already been fixed in buffered neutral 10% formalin. A preliminary diagnosis can be made by examining Giemsa-stained impression smears of affected tissues (Figs. 1, 4 and 10). *T. gondii* tachyzoites in smears are crescentic to globular, depending on the stage of division (Figs. 1, 4 and 10). However, in histologic sections tachyzoites are globular to oval and about half of the size of those in smears (Fig. 6).

Immunohistochemical staining with *T. gondii* specific antibodies can aid diagnosis (Fig. 9). Polyclonal antibodies raised against whole parasites are often superior to monoclonal

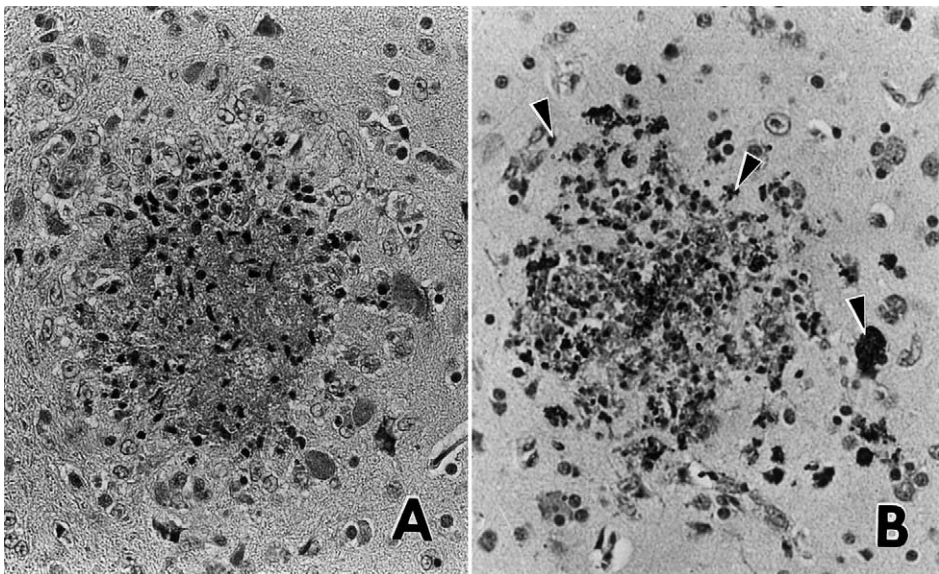


Fig. 9. Adjacent sections of cerebrum of an experimentally-infected budgerigar 14 days after feeding oocysts: (A) numerous tachyzoites are present, but are not visible (H and E); (B) immunohistochemical staining with anti-*T. gondii* antibodies; all black spots (arrowheads) are tachyzoites.

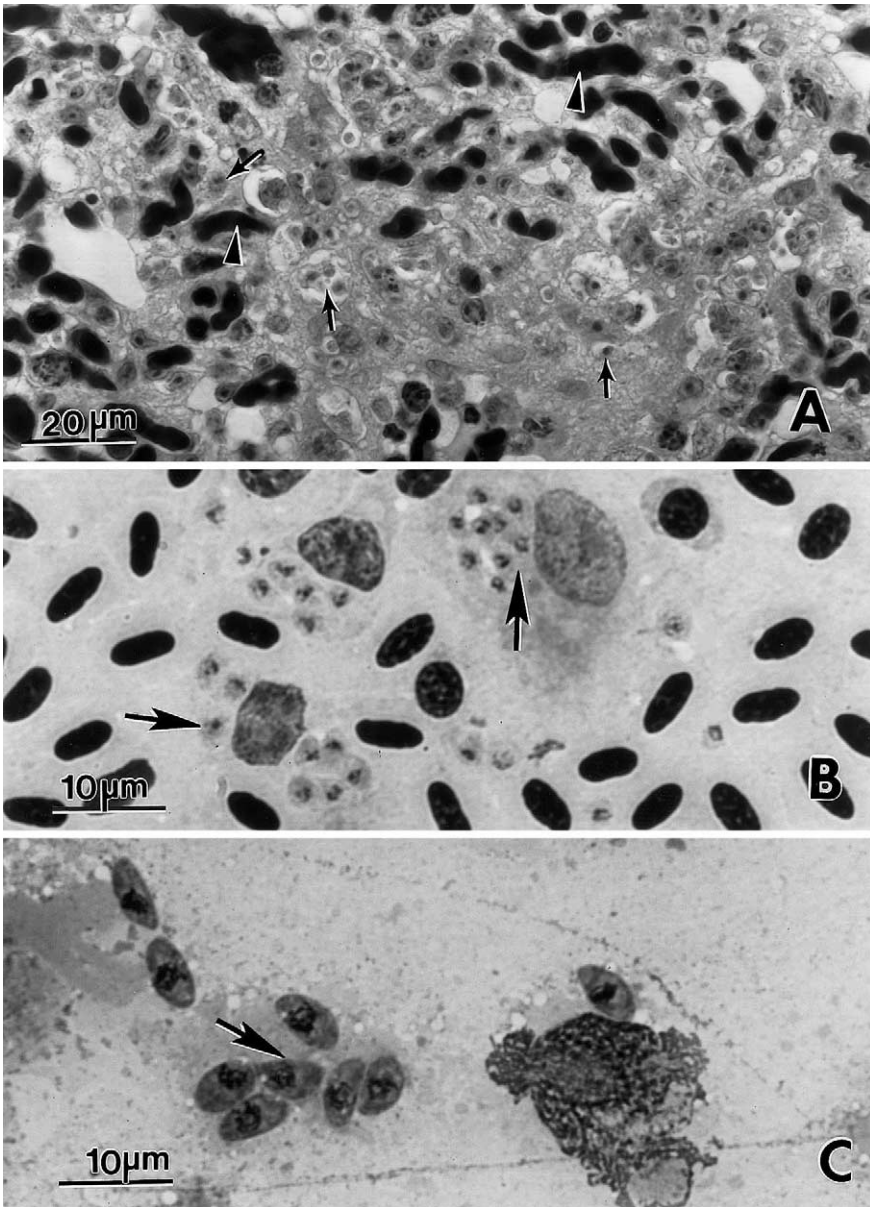


Fig. 10. *Atoxoplasma* and *Toxoplasma* compared in tissues of birds: (A) histologic section of the lung of a naturally-infected mynah. Small merozoites (arrows) are present in an area of necrosis. The dark areas are capillaries (arrowheads). *Atoxoplasma* often stain fainter than host cells and are difficult to identify in sections stained with H and E. (B) Impression smear of lung of the mynah in Fig. 10A. Note numerous tachyzoites (arrows) (Giemsa); (C) impression smear of intestine of a budgerigar infected with *T. gondii* (Giemsa). Compare the size of *T. gondii* tachyzoites in this figure with merozoites in Fig. 10B.





Fig. 11. Transmission electron micrograph of *Atoxoplasma* sp. merozoites in the liver of a naturally-infected mynah. Note one uninucleate merozoite (large arrow) with a prominent nucleus (N), a few small rhoptries (R) toward the conoidal (C) end. Most micronemes (M) are present anterior to the nucleus and micronemes are often arranged in rows. Also note one merozoite (arrowheads) with two well defined undivided nuclei (N); such a stage is absent in *T. gondii* tachyzoites.

antibodies for immunohistochemical diagnosis of toxoplasmosis in tissue sections. Preservation of tissues in 10% formalin does not affect the immunohistochemical reaction. *T. gondii* tissue cysts are often globular, have a thin cyst wall ( $<0.5\text{ }\mu\text{m}$ ) and contain small (about  $5\text{ }\mu\text{m}$ ), slender bradyzoites (Fig. 4B). The bradyzoites are periodic acid Schiff (PAS) positive and there are no intracystic septa (Dubey and Beattie, 1988).

*Atoxoplasma* and *Sarcocystis* are two parasite genera that should be considered in the differential diagnosis of avian toxoplasmosis. *Atoxoplasma* spp. are considered common parasites of passerine birds (Baker et al., 1972; Levine, 1982) and have a fecal-oral cycle with extraintestinal stages in visceral tissues of birds, especially the liver and spleen. Proliferative stages (merozoites) of *Atoxoplasma* sp. are smaller than *T. gondii* tachyzoites, both in smears and in histologic sections (Fig. 10).

Ultrastructurally, *Atoxoplasma* merozoites divide by schizogony, have small vestigial rhoptries, and small numbers of micronemes (Fig. 11). There are no tissue cysts, and *Atoxoplasma* does not react with *T. gondii* antibodies. There are no antibodies available for immunohistochemical diagnosis of atoxoplasmosis because the parasite has not yet been isolated in cell culture or in laboratory animals. In addition, other parasites related to *Atoxoplasma* may be found in birds (Baker et al., 1996). A *Lankesterella*-like coccidian was found to cause respiratory distress in cardinals (*Cardinalis cardinalis*) in California, USA (Baker

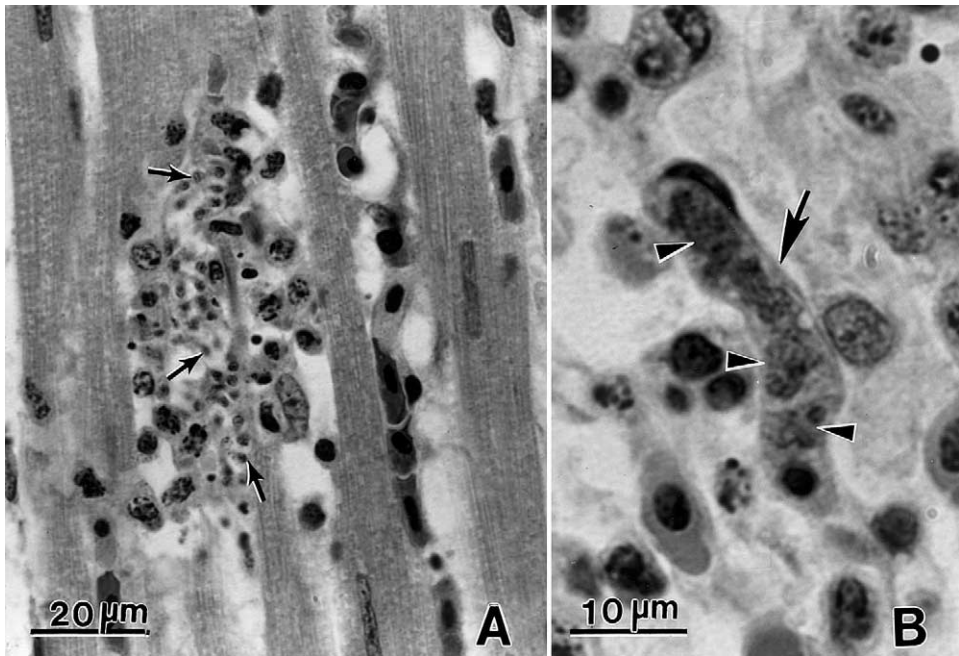


Fig. 12. Section of heart (A) and lung (B) from the capercaillie from Finland with *Sarcocystis* infection (H and E). (A) Note many merozoites (arrows) and inflammatory cells in a focus of myocardial necrosis. These merozoites are difficult to distinguish from *T. gondii* tachyzoites by light microscopy. (B) Note an elongated immature schizont (arrow) with lobed nucleus (arrowheads).

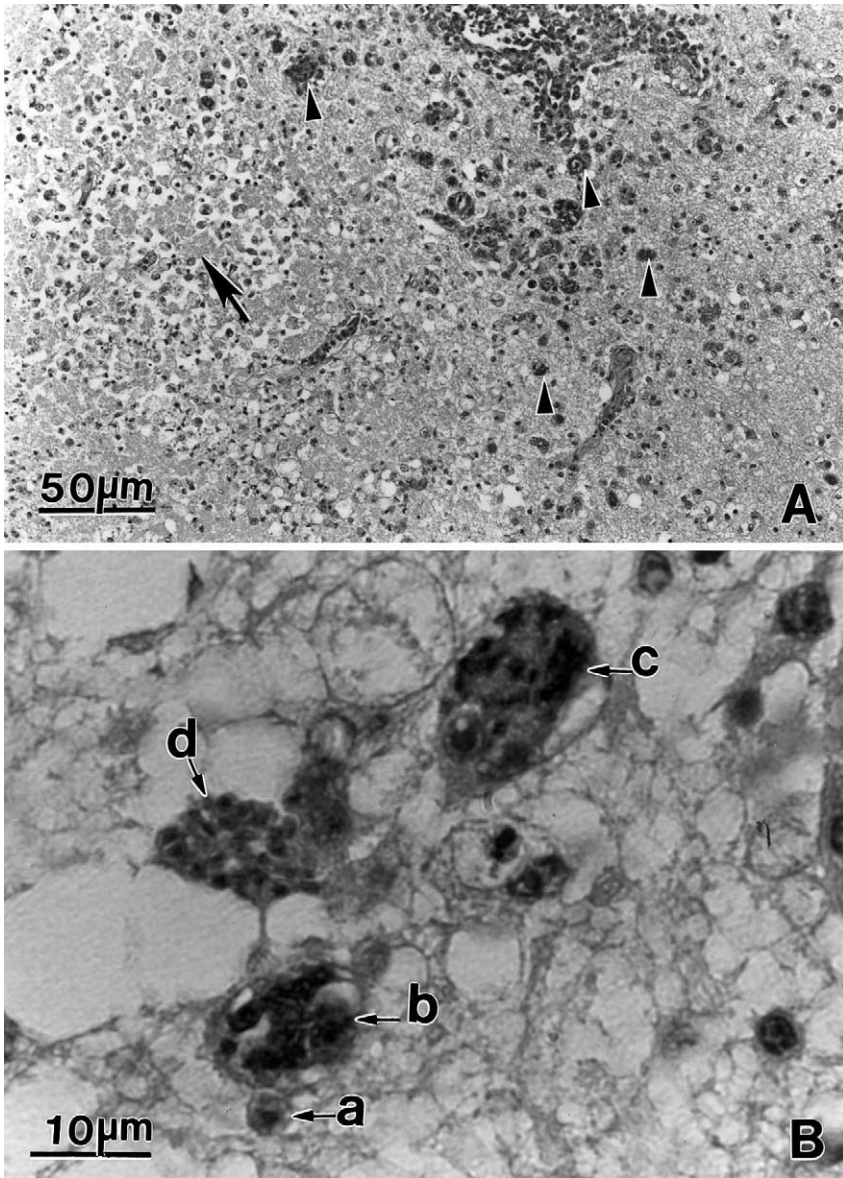


Fig. 13. Sections of brain of an ibis (*Carphibis spinicollis*) naturally-infected with a *Sarcocystis neurona*-like organism (H and E). (A) Note focal necrosis with macrophage infiltration (arrow) and numerous schizonts (arrow-heads). (B) Focal necrosis without inflammation and developing stages of schizonts: (a) small uninucleate schizont; (b) schizont with a lobed nucleus, (c) schizont with merozoite formation, and (d) schizont with merozoites.

et al., 1996; Speer et al., 1997). Asexual and sexual stages were found associated with pulmonic lesions. Some schizonts were found intravascularly. Male and female gamonts, and sporulated oocysts were present in lung parenchyma.

*Sarcocystis* spp. (*S. falcatula* or *S. falcatula*-like) can cause generalized disease in birds, especially in passerines and psittacines (Smith et al., 1989; Hillyer et al., 1991). Pneumonia is the predominant lesion of acute *S. falcatula* infection and disease is associated with intravascular development of *S. falcatula* schizonts (Smith et al., 1989).

Occasionally, certain unidentified species of *Sarcocystis* can cause neural and myocardial sarcocystosis associated with development of *Sarcocystis* schizonts in affected tissues (Gustafsson et al., 1997; Dubey et al., 2001c). Affected birds may die acutely or have a chronic disease. Clinical signs include ataxia, fearlessness, twisting of neck and blindness. In neural sarcocystosis, lesions and schizonts are often confined to the CNS. Neural sarcocystosis, simulating toxoplasmosis, has been reported in a goshawk (*Accipiter gentilis atricapillus*), turkeys, capercaillie (*T. urogallus*) (Fig. 12), an ibis (*Carphibis spinicollis*) (Fig. 13) and an eagle (*Aquila chrysaetos*) (Aguilar et al., 1991; Dubey et al., 1991; Teglas et al., 1998; Dubey et al., 2000a, 2001c).

Although *Sarcocystis* merozoites (Fig. 12) may resemble *T. gondii* tachyzoites, search for developing stages (Fig. 3) is helpful in diagnosis.

*Sarcocystis* schizonts divide by a specialized form of schizogony where the parasite becomes multilobed (Fig. 13B) and eventually four or more merozoites are produced, whereas *T. gondii* divides into two zotes. Ultrastructure examination also helps diagnosis. Unlike *T. gondii* or *Atoxoplasma*, *Sarcocystis* spp. merozoites lack rhoptries (Dubey et al., 1989). Immunohistochemical examination using *Sarcocystis*-specific antibodies can aid diagnosis (Dubey et al., 2001a,b).

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## References

- Adie, J.R., 1908. Note on a parasite in the sparrow. Indian Med. Gaz. 43, 176–180.
- Aguilar, R.F., Shaw, D.P., Dubey, J.P., Redig, P., 1991. *Sarcocystis*-associated encephalitis in an immature northern goshawk (*Accipiter gentilis atricapillus*). J. Zoo Wildl. Med. 22, 466–469.
- Alosi, C., Iannuzzi, L., 1966. Toxoplasmosi acuta spontanea dei colombi. Segnalazione di un focolaio a Messina. Acta Med. Vet. 12, 265–273.
- Aragão, H.B., 1911. Observações sobre algumas hemogregarinas das aves. Mem. Inst. Oswaldo Cruz 3, 54–64.
- Arene, F.O.I., 1999. Seroprevalence of *Toxoplasma gondii* in vultures (*Pseudogyps africanus*) from eastern Nigeria. Acta Parasitol. 44, 79–80.
- Baker, J.R., Bennett, G.F., Clark, G.W., Laird, M., 1972. Avian blood coccidians. Adv. Parasitol. 10, 1–30.
- Baker, D.G., Speer, C.A., Yamaguchi, A., Griffey, S.M., Dubey, J.P., 1996. An unusual coccidian parasite causing pneumonia in a northern cardinal (*Cardinalis cardinalis*). J. Wildl. Dis. 32, 130–132.
- Beyer, T.V., Shevkunova, E.A., 1986. A review of toxoplasmosis of animals in the USSR. Vet. Parasitol. 19, 225–243.

- Biancifiore, F., Rondini, C., Grelloni, V., Frescura, T., 1986. Avian toxoplasmosis: experimental infection of chicken and pigeon. *Comp. Immunol. Microbiol. Infect. Dis.* 9, 337–346.
- Boehringer, E.G., Fornari, O.E., Boehringer, I.K., 1962. The first case of *Toxoplasma gondii* in domestic ducks in Argentina. *Avian Dis.* 6, 391–396.
- Burridge, M.J., Bigler, W.J., Forrester, D.J., Hennemann, J.M., 1979. Serologic survey for *Toxoplasma gondii* in wild animals in Florida. *J. Am. Vet. Med. Assoc.* 175, 964–967.
- Carini, A., 1911. Infection spontanée du pigeon et du chien due au *Toxoplasma cuniculi*. *Bull. Soc. Pathol. Exot.* 4, 518–519.
- Carini, A., Maciel, J., 1913. Toxoplasmose natural do cão. *Rev. Vet. Zootec.* 3, 374–375.
- Cassamagnaghi, A., Bianchi Bazerque, A., Scelza, R., Ferrando, H., 1952. La toxoplasmosis. Su incorporación en la patología Uruguaya. Reconocimiento de dos cepas en nuestras aves domésticas. Su transmisión y carácter infeccioso para los mamíferos. *Boll. Ministerio de Agric. y Ganadería Montevideo* 33, 34–38.
- Cassamagnaghi, A., Bianchi Bazerque, A., Scelza, R., Ferrando, H., 1977. La toxoplasmosis. Su incorporación en la patología Uruguaya. *An. Fac. Veterinaria (Uruguay)* 1, 27–47.
- Čatár, G., 1974. Toxoplazmóza v ekologických podmienkach na Slovensku (in Slovakian). *Biologické Práce (Bratislava)* 20, 1–138.
- Ceruti Sola, S., Parenti, E., Turilli, C., 1985. Verhandlungsbericht des 27. Internationalen Symposiums über die Erkrankungen der Zootiere, 9–13 June. pp. 355–358.
- Choi, W.Y., Yoo, J.E., Nam, H.W., Oh, C.Y., Kim, S.W., Katakura, K., Kobayashi, A., 1987. *Toxoplasma* antibodies by indirect latex agglutination tests in zoo animals. *Korean J. Parasitol.* 25, 13–23.
- Cotteleer, C., Famerée, L., 1978. Parasites intestinaux et anticorps antitoxoplasmiques chez les colombins en Belgique. *Schweiz. Arch. Tierheilkd.* 120, 181–187.
- Coutelen, F., Biguet, J., Doby, J.M., Deblock, S., 1953. Le problème des toxoplasmoses aviaires. Réceptivité variable de quelques oiseaux à une souche humaine de toxoplasmes. *Ann. Parasitol. Hum. Comp.* 28, 129–156.
- de Mello, F., 1915. Preliminary note on a new haemogregarine found in the pigeon's blood. *Indian J. Med. Res.* 3, 93–94.
- de Mello, F., 1935. On a toxoplasmid of *Fulica atra* L. with special reference to a probable sexuality of agametes. *Proc. Indian Acad. Sci.* 1, 705–709.
- Dhillon, A.S., Thacker, H.L., Winterfield, R.W., 1982. Toxoplasmosis in mynahs. *Avian Dis.* 26, 445–449.
- Drobeck, H.P., Manwell, R.D., Bernstein, E., Dillon, R.D., 1953. Further studies of toxoplasmosis in birds. *Am. J. Hyg.* 58, 329–339.
- Dubey, J.P., Beattie, C.P., 1988. *Toxoplasmosis of Animals and Man*. CRC Press, Boca Raton, Florida, 220 pp.
- Dubey, J.P., Odening, K., 2001. Toxoplasmosis and related infections. In: Samuel, B., Pybur, M., Kocan, A.M. (Eds.), *Parasitic Diseases of Wild Mammals*. Iowa State University Press, Ames, pp. 478–519.
- Dubey, J.P., Hamir, A.N., 2002. Experimental toxoplasmosis in budgerigars (*Melopsittacus undulatus*). *J. Parasitol.* 88, in press.
- Dubey, J.P., Speer, C.A., Fayer, R., 1989. *Sarcocystosis of Animals and Man*. CRC Press, Boca Raton, Florida, 215 pp.
- Dubey, J.P., Porter, S.L., Hattel, A.L., Kradel, D.C., Topper, M.J., Johnson, L., 1991. Sarcocystosis-associated clinical encephalitis in a golden eagle (*Aquila chrysaetos*). *J. Zoo Wildl. Med.* 22, 233–236.
- Dubey, J.P., Porter, S.L., Tseng, F., Shen, S.K., Thulliez, P., 1992. Induced toxoplasmosis in owls. *J. Zoo Wildl. Med.* 23, 98–102.
- Dubey, J.P., Camargo, M.E., Ruff, M.D., Wilkins, G.C., Shen, S.K., Kwok, O.C.H., Thulliez, P., 1993a. Experimental toxoplasmosis in turkeys. *J. Parasitol.* 79, 949–952.
- Dubey, J.P., Ruff, M.D., Kwok, O.C.H., Shen, S.K., Wilkins, G.C., Thulliez, P., 1993b. Experimental toxoplasmosis in Bobwhite quail (*Colinus virginianus*). *J. Parasitol.* 79, 935–939.
- Dubey, J.P., Goodwin, M.A., Ruff, M.D., Kwok, O.C.H., Shen, S.K., Wilkins, G.C., Thulliez, P., 1994a. Experimental toxoplasmosis in Japanese quail. *J. Vet. Diagn. Invest.* 6, 216–221.
- Dubey, J.P., Ruff, M.D., Wilkins, G.C., Shen, S.K., Kwok, O.C.H., 1994b. Experimental toxoplasmosis in pheasants (*Phasianus colchicus*). *J. Wildl. Dis.* 30, 40–45.
- Dubey, J.P., Goodwin, M.A., Ruff, M.D., Shen, S.K., Kwok, O.C.H., Wilkins, G.L., Thulliez, P., 1995. Experimental toxoplasmosis in chukar partridges (*Alectoris graeca*). *Avian Pathol.* 24, 95–107.
- Dubey, J.P., Rudbäck, E., Topper, M.J., 1998. Sarcocystosis in capercaillie (*Tetrao urogallus*) in Finland: description of the parasite and lesions. *J. Parasitol.* 84, 104–108.

- Dubey, J.P., Quist, C.F., Fritz, D., 2000a. Systematic sarcocystosis in a turkey. *J. Wildl. Dis.* 36, 755–760.
- Dubey, J.P., Scandrett, W.B., Kwok, O.C.H., Gajadhar, A.A., 2000b. Prevalence of antibodies to *Toxoplasma gondii* in ostriches (*Struthio camelus*). *J. Parasitol.* 86, 623–624.
- Dubey, J.P., Garner, M.M., Willette, M.M., Batey, K.L., Gardiner, C.H., 2001a. Disseminated toxoplasmosis in magpie geese (*Anseranas semipalmata*) with large numbers of tissue cysts in livers. *J. Parasitol.* 87, 219–223.
- Dubey, J.P., Garner, M.M., Stetter, M.D., Marsh, A.E., Barr, B.C., 2001b. Acute *Sarcocystis falcatula*-like infection in a carmine bee-eater (*Merops nubicus*) and immunohistochemical cross reactivity between *Sarcocystis falcatula* and *Sarcocystis neurona*. *J. Parasitol.* 87, 824–832.
- Dubey, J.P., Johnson, G.C., Bermudez, A., Suedmeyer, K.W., Fritz, D.L., 2001c. Neural sarcocystosis in a straw-necked ibis (*Carphibis spinicollis*) associated with a *Sarcocystis neurona*-like organism and description of muscular sarcocysts of an unidentified *Sarcocystis* species. *J. Parasitol.* 87, 1317–1322.
- Feldman, H.A., Sabin, A.B., 1949. Skin reactions to toxoplasmic antigen in people of different ages without known history of infection. *Pediatrics* 4, 798–804.
- Finlay, P., Manwell, R.D., 1956. *Toxoplasma* from the crow, a new natural host. *Exp. Parasitol.* 5, 149–153.
- Franti, C.E., Connolly, G.E., Riemann, H.P., Behymer, D.E., Ruppner, R., Willadsen, C.M., Longhurst, W., 1975. A survey for *Toxoplasma gondii* antibodies in deer and other wildlife on a sheep range. *J. Am. Vet. Med. Assoc.* 167, 565–568.
- Franti, C.E., Riemann, H.P., Behymer, D.E., Suther, D., Howarth, J.A., Ruppner, R., 1976. Prevalence of *Toxoplasma gondii* antibodies in wild and domestic animals in northern California. *J. Am. Vet. Med. Assoc.* 169, 901–906.
- Frenkel, J.K., 1953. Host, strain and treatment variation as factors in the pathogenesis of toxoplasmosis. *Am. J. Trop. Med. Hyg.* 2, 390–415.
- Frenkel, J.K., 1981. False-negative serologic tests for *Toxoplasma* in birds. *J. Parasitol.* 67, 952–953.
- Frenkel, J.K., Hassanein, K.M., Hassanein, R.S., Brown, E., Thulliez, P., Quintero-Nunez, R., 1995. Transmission of *Toxoplasma gondii* in Panama City, Panama: a 5-year prospective cohort study of children, cats, rodents, birds, and soil. *Am. J. Trop. Med. Hyg.* 53, 458–468.
- Galli-Valerio, B., 1939. Sur une toxoplasmiose du *Melopsittacus undulatus* Shaw. *Schweiz. Arch. Tierheilkd.* 81, 458–460.
- Gibbens, J.C., Abraham, E.J., MacKenzie, G., 1997. Toxoplasmosis in canaries in Great Britain. *Vet. Rec.* 140, 370–371.
- Gibson, C.L., Eyles, D.E., 1957. *Toxoplasma* infections in animals associated with a case of human congenital toxoplasmosis. *Am. J. Trop. Med. Hyg.* 6, 990–1000.
- Gustafsson, K., Book, M., Dubey, J.P., Ugglä, A., 1997. Meningoencephalitis in capercaillie (*Tetrao urogallus* L.) caused by a *Sarcocystis*-like organism. *J. Zoo Wildl. Dis.* 28, 280–284.
- Hartley, W.J., Dubey, J.P., 1991. Fatal toxoplasmosis in some native Australian birds. *J. Vet. Diagn. Invest.* 3, 167–169.
- Haslett, T.M., Schneider, W.J., 1978. Occurrence and attempted transmission of *Toxoplasma gondii* in European starlings (*Sturnus vulgaris*). *J. Wildl. Dis.* 14, 173–175.
- Hegner, R., Wolfson, F., 1938a. *Toxoplasma*-like parasites in canaries infected with *Plasmodium*. *Am. J. Hyg.* 27, 212–220.
- Hegner, R., Wolfson, F., 1938b. Association of *Plasmodium* and *Toxoplasma*-like parasites in birds. *Am. J. Hyg.* 28, 437–454.
- Hejlíček, K., Prošek, F., Tremel, F., 1981. Isolation of *Toxoplasma gondii* in free-living small mammals and birds. *Acta Vet. Brno.* 50, 233–236.
- Herman, C.M., 1937. *Toxoplasma* in North American birds and attempted transmission to canaries and chickens. *Am. J. Hyg.* 25, 303–312.
- Hillyer, E.V., Anderson, M.P., Greiner, E.C., Atkinson, C.T., Frenkel, J.K., 1991. An outbreak of *Sarcocystis* in a collection of psittacines. *J. Zoo Wildl. Med.* 22, 434–445.
- Holst, I., Chinchilla, M., 1990. Development and distribution of cysts of an avirulent strain of *Toxoplasma* and the humoral immune response in mice. *Rev. Biol. Trop.* 38, 189–193.
- Howerth, E.W., Rodenroth, N., 1985. Fatal systemic toxoplasmosis in a wild turkey. *J. Wildl. Dis.* 21, 446–449.
- Howerth, E.W., Rich, G., Dubey, J.P., Yogasundram, K., 1991. Fatal toxoplasmosis in a red lory (*Eos bornea*). *Avian Dis.* 35, 642–646.

- Hubbard, G., Witt, W., Healy, M., Schmidt, R., 1986. An outbreak of toxoplasmosis in zoo birds. *Vet. Pathol.* 23, 639–641.
- Hülphers, G., Lilleengen, K., Rubarth, S., 1947. Toxoplasmos hos hare och tjäder. *Sv. Vet. Tidskr.* 52, 295–332.
- Ippen, R., Kozojed, V., Jíra, J., 1981. Toxoplasmosis in zoo animals. *Folia Parasitologica (Praha)* 28, 109–115.
- Jacobs, L., Melton, M.L., Jones, F.E., 1952. The prevalence of toxoplasmosis in wild pigeons. *J. Parasitol.* 38, 457–461.
- Jacobs, L., Melton, M.L., Cook, M.K., 1953. Experimental toxoplasmosis in pigeons. *Exp. Parasitol.* 2, 403–416.
- Jygiste, A.K., Gusev, V.M., 1962. On toxoplasmosis of wild birds in USSR (in Russian). *Dokl. Acad. Sci. USSR, Earth Sci. Sect.* 143, 491–492.
- Johnson, C.M., 1943. Immunological and epidemiological investigation under the direction of C.M. Johnson, protozoologist, Annual Report of the Gorgas Memorial Laboratory, pp. 15–16.
- Kageruka, P., Willaert, E., 1971. *Toxoplasma gondii* (Nicolle et Manceaux 1908) isole chez *Goura cristata* Pallas et *Manis crassicaudata* Geoffroy. *Acta Zool. Pathol. Antverp.* 52, 3–10.
- Kirkpatrick, C.E., Colvin, B.A., Dubey, J.P., 1990. *Toxoplasma gondii* antibodies in common barn-owls (*Tyto alba*) and pigeons (*Columba livia*) in New Jersey. *Vet. Parasitol.* 36, 177–180.
- Lainson, R., 1955. Toxoplasmosis in England II. Variation factors in the pathogenesis of *Toxoplasma* infections: the sudden increase in virulence of a strain after passage in multimammate rats and canaries. *Ann. Trop. Med. Parasitol.* 49, 397–416.
- Laveran, A., 1900. Au sujet de l'hématozoaire endoglobulaire de *Padda oryzivora*. *Comp. Rend. Soc. Biol. Paris* 52, 19–20.
- Laveran, A., Marullaz, M., 1913. Recherches expérimentales sur le *Toxoplasma gondii*. *Bull. Soc. Pathol. Exot.* 6, 460–468.
- Levine, N.D., 1977. Taxonomy of *Toxoplasma*. *J. Protozool.* 24, 36–41.
- Levine, N.D., 1982. The genus *Atoxoplasma* (Protozoa, Apicomplexa). *J. Parasitol.* 68, 719–723.
- Lindsay, D.S., Dubey, J.P., Blagburn, B.L., 1991. *Toxoplasma gondii* infections in red-tailed hawks inoculated orally with tissue cysts. *J. Parasitol.* 77, 322–325.
- Lindsay, D.S., Smith, P.C., Hoerr, F.J., Blagburn, B.L., 1993. Prevalence of encysted *Toxoplasma gondii* in raptors from Alabama. *J. Parasitol.* 79, 870–873.
- Lindsay, D.S., Smith, P.C., Blagburn, B.L., 1994. Prevalence and isolation of *Toxoplasma gondii* from wild turkeys in Alabama. *J. Helminthol. Soc. Wash.* 61, 115–117.
- Lindsay, D.S., Gasser, R.B., Harrigan, K.E., Madill, D.N., Blagburn, B.L., 1995. Central nervous system toxoplasmosis in roller canaries. *Avian Dis.* 39, 204–207.
- Literák, I., Hejlíček, K., Nezval, J., Folk, C., 1992. Incidence of *Toxoplasma gondii* in populations of wild birds in the Czech Republic. *Avian Pathol.* 21, 659–665.
- Literák, I., Pinowski, J., Anger, M., Juřicová, Z., Kyu-Hwang, H., Romanowski, J., 1997. *Toxoplasma gondii* antibodies in house sparrows (*Passer domesticus*) and tree sparrows (*P. montanus*). *Avian Pathol.* 26, 823–827.
- Literák, I., Sedlák, K., Juřicová, Z., Pavlásek, I., 1999. Experimental toxoplasmosis in house sparrows (*Passer domesticus*). *Avian Pathol.* 28, 363–368.
- Mandelli, G., Persiani, G., 1966. Ricerche sierologiche sulla presenza e diffusione della toxoplasmosi nei piccioni torraoli (*Columba livia*). *Clin. Vet. (Milano)* 89, 161–166.
- Manwell, R.D., 1941. Avian toxoplasmosis with invasion of the erythrocytes. *J. Parasitol.* 27, 245–251.
- Manwell, R.D., Drobeck, H.P., 1951. Mammalian toxoplasmosis in birds. *Expt. Parasitol.* 1, 83–93.
- Manwell, R.D., Coulston, F., Binckley, E.C., Jones, V.P., 1945. Mammalian and avian *Toxoplasma*. *J. Infect. Dis.* 76, 1–14.
- Marullaz, M., 1913. Au sujet d'un toxoplasme des oiseaux. *Bull. Soc. Pathol. Exot.* 6, 323–326.
- Mason, R.W., Hartley, W.J., Dubey, J.P., 1991. Lethal toxoplasmosis in a little penguin (*Eudyptula minor*) from Tasmania. *J. Parasitol.* 77, 328.
- Mikaelian, I., Dubey, J.P., Martineau, D., 1997. Severe hepatitis resulting from toxoplasmosis in a barred owl (*Strix varia*) from Québec, Canada. *Avian Dis.* 41, 738–740.
- Miller, N.L., Frenkel, J.K., Dubey, J.P., 1972. Oral infections with *Toxoplasma* cysts and oocysts in felines, other mammals, and in birds. *J. Parasitol.* 58, 928–937.
- Murata, K., 1989. A serological survey of *Toxoplasma gondii* infection in zoo animals and other animals. *Jpn. J. Vet. Sci.* 51, 935–940.

- Mushi, E.Z., Binta, M.G., Chabo, R.G., Ndebele, R., Panzirah, R., 2001. Seroprevalence of *Toxoplasma gondii* and *Chlamydia psittaci* in domestic pigeons (*Columba livia domestica*) at Sebele, Gaborone, Botswana. Onderstepoort J. Vet. Res. 68, 159–161.
- Nicolau, S., Kopciowska, L., 1935. Toxoplasmose spontanée du chien. Bull. Soc. Pathol. Exot. 28, 490–498.
- Niederehe, H., 1964. Toxoplasma-Infektion bei verwilderten Tauben. Tierärztl. Umschau. 19, 256–257.
- Nóbrega, P., Reis, J., 1942. Identidade dos toxoplasmos de aves e de mamíferos. Arq. Insti. Biol. (São Paulo) 13, 21–28.
- Orosz, S.E., Mullins, J.D., Patton, S., 1992. Evidence of toxoplasmosis in two ratites. J. Assoc. Avian Vet. 6, 219–222.
- Paasch, L.M., 1983. Toxoplasmosis en palomas. Vet. Méx. 14, 39–41.
- Pak, S.M., 1970. A strain of *Toxoplasma gondii* SHP isolated from the common tern (*Sterna hirundo*) (in Russian). Voprosy Prirodnoi Ochagovosti Boleznij (Alma-Ata). Contributions on the Natural Nidality of Diseases 3, 49.
- Pak, S.M., 1971. Susceptibility of birds and rodents to avirulent strains of *Toxoplasma* isolated from sparrows (in Russian). Voprosy prirodnoi ochagovosti boleznej (Alma-Ata). Contributions Nat. Nidality Dis. 4, 78–94.
- Pak, S.M., 1972. Toxoplasmosis of sparrows (in Russian). Contributions Nat. Nidality Dis. 5, 116–125.
- Pak, S.M., 1974. Vosprimchivost ptic k zarazheniu zigocistami toksoplazm. Voprosy prirodnoi ochagovosti boleznej (Alma-Ata). In: Galuzo, I.G. (Ed.), Zhiznennyi Tsikl Toksoplazm. Publishing House Nauka, Alma-Ata, pp. 121–126.
- Pak, S.M., 1976. Toxoplasmosis of birds in Kazakhstan (in Russian). Nauka Publishing, Alma-Ata, 115 pp.
- Parenti, E., Cerruti Sola, S., Turilli, C., Corazzola, S., 1986. Spontaneous toxoplasmosis in canaries (*Serinus canaria*) and other small passerine cage birds. Avian Pathol. 15, 183–197.
- Partington, C.J., Gardiner, C.H., Fritz, D., Phillips, L.G., Montali, R.J., 1989. Attoxoplasmosis in Bali mynahs (*Leucopsar rothschildi*). J. Zoo Wildl. Med. 20, 328–335.
- Pendergraph, G.E., 1972. A serological study of toxoplasmosis in wild pigeons and their possible role in its dissemination. J. Elisha Mitchell Sci. Soc. 88, 208–209.
- Pires, W., Santos, V.D., 1934. Lesões histo-patológicas observadas num caso de toxoplasmose natural do pombo. Rev. Dept. Fac. Prod. Anim. 1, 19–23.
- Pixell, H.L.M., 1913. Notes on *Toxoplasma gondii*. Proc. R. Soc. B. 87, 67–77.
- Plimmer, H.G., 1915. Report on the deaths which occurred in the zoological gardens during 1914, together with a list of the blood-parasites found during the year. Proc. Zool. Soc. London 88, 123–130.
- Plimmer, H.G., 1916. Notes on the genus *Toxoplasma* with a description of three new species. Proc. R. Soc. B. 89, 291–296.
- Poelma, F.G., Zwart, P., 1972. Toxoplasmose bij kroonduiven en andere vogels in de Koninklijke Rotterdamse Dieggaarde (Blijdorp). Acta Zool. Pathol. Antverp. 55, 29–40.
- Pokorný, B., 1955. Přspěvek k poznání toxoplasmosy polní zvěře. Cesk. Parasitol. 2, 157–160.
- Quist, C.F., Dubey, J.P., Luttrell, M.P., Davidson, W.R., 1995. Toxoplasmosis in wild turkeys: a case report and serologic survey. J. Wildl. Dis. 31, 255–258.
- Raffaele, G., 1932. Sulla cosiddette toxoplasmosi dei passeri. Riv. Malariol. 11, 825–838.
- Ratcliffe, H.L., Worth, C.B., 1951. Toxoplasmosis of captive wild birds and mammals. Am. J. Pathol. 27, 655–667.
- Reis, J., Nóbrega, P., 1936. Toxoplasmose. Tratado de doenças das aves, Proc. Ed. Inst. Biológico (São Paulo), pp. 302–306.
- Rodríguez, J.D., 1954. Toxoplasmosis. Experiencias con una cepa de *Toxoplasma* de origen aviario. Rev. Ecuador Hig. Med. Trop. 11, 1–11.
- Ruiz, A., Frenkel, J.K., 1980. Intermediate and transport hosts of *Toxoplasma gondii* in Costa Rica. Am. J. Trop. Med. Hyg. 29, 1161–1166.
- Sabin, A.B., Feldman, H.A., 1948. Dyes as microchemical indicators of a new immunity phenomenon affecting a protozoon parasite (*Toxoplasma*). Science 108, 660–663.
- Schulte, F., 1954. Toxoplasmose-Encephalitis beim Geflügel. Deut. Tierärztl. Wochschr. 61, 482–484.
- Sedlák, K., Literák, I., Vitula, F., Benák, J., 2000. High susceptibility of partridges (*Perdix perdix*) to toxoplasmosis compared with other gallinaceous birds. Avian Pathol. 29, 563–569.
- Siim, J.C., Biering-Sørensen, U., Møller, T., 1963. Toxoplasmosis in domestic animals. Adv. Vet. Sci. 8, 335–429.
- Simitch, T., Petrovitch, Z., Bordjocki, A., Tomanovitch, B., 1959. Contribution à la connaissance de la virulence de *Toxoplasma gondii* pour *Carduelis carduelis* L. Arch. Institut. Pasteur Algér. 37, 409–411.



- Simitch, T., Bordjocki, A., Petrovitch, Z., Tomanovitch, B., Savin, Z., 1961. La toxoplasmose des oiseaux. I. L'infection naturelle de la volaille domestique par *Toxoplasma gondii* en Yougoslavie. Arch. Inst. Pasteur Algér. 39, 135–139.
- Simitch, T., Bordjocki, A., Savin, Z., 1963. Infection du canard per os, par la forme kystique de *Toxoplasma gondii*. Rec. Méd. Vét. 139, 403–406.
- Simitch, T., Petrovitch, Z., Bordjocki, A., Savin, Z., Mikovitch, Z., 1965. Infection expérimentale de la caille (*Coturnix coturnix* L.) per os, avec la forme végétative et la forme kystique de *Toxoplasma gondii*. Bull. Acad. Vét. France 38, 27–29.
- Smith, J.H., Neill, P.J.G., Box, E.D., 1989. Pathogenesis of *Sarcocystis falcatula* (Apicomplexa: Sarcocystidae) in the budgerigar (*Melopsittacus undulatus*). III. Pathologic and quantitative parasitologic analysis of extrapulmonary disease. J. Parasitol. 75, 270–287.
- Speer, C.A., Baker, D.G., Yamaguchi, A., Dubey, J.P., 1997. Ultrastructural characteristics of a *Lankesterella*-like coccidian causing pneumonia in a northern cardinal (*Cardinalis cardinalis*). Acta Protozool. 36, 39–47.
- Springer, L., 1942. Toxoplasmose epizootica entre pombos. Arq. Biol. (São Paulo) 26, 74–76.
- Tackaert-Henry, M.C., Kageruka, P., 1977. Une épizootie de toxoplasmose parmi les pigeons couronnés, *Goura cristata* Pallas et *Goura victoria* Frazer, du Zoo d'Anvers. Acta Zool. Pathol. Antverp. 69, 163–168.
- Taddia, L., 1938. Plasmodi e corpi *Toxoplasma* simili nei passerii del éneto. Riv. Malariol. 17, 237–241.
- Taddia, L., Valentino, D., 1939. Ricerche sugli emoparassiti degli uccelli del Veneto. Archivis Italiani di Scienze Mediche Colonisli 20, 637–656.
- Teglas, M.B., Little, S.E., Latimer, K.S., Dubey, J.P., 1998. *Sarcocystis*-associated encephalitis and myocarditis in a wild turkey (*Meleagris gallopavo*). J. Parasitol. 84, 661–663.
- Vickers, M.C., Hartley, W.J., Mason, R.W., Dubey, J.P., Schollam, L., 1992. Blindness associated with toxoplasmosis in canaries. J. Am. Vet. Med. Assoc. 200, 1723–1725.
- Vogelsang, E.G., Gallo, P., 1954. Toxoplasmosis en aves de Venesuela. Rev. Med. Vet. Parasitol. (Caracas) 13, 59–61.
- Wallace, G.D., 1973. Intermediate and transport hosts in the natural history of *Toxoplasma gondii*. Am. J. Trop. Med. Hyg. 22, 456–464.
- Wiktor, T.J., 1950. Toxoplasmose animale. Sur une épidémie des lapins et des pigeons a Stanleyville (Congo Belge). Ann. Soc. Belg. Med. Trop. 30, 97–107.
- Williams, S.M., Fulton, R.M., Render, J.A., Mansfield, L., Bouldin, M., 2001. Ocular and encephalic toxoplasmosis in canaries. Avian Dis. 45, 262–267.
- Wolfson, F., 1941. Mammalian *Toxoplasma* in erythrocytes of canaries, ducks, and duck embryos. Am. J. Trop. Med. Hyg. 21, 653–658.
- Work, T.M., Massey, J.F., Lindsay, D., Dubey, J.P., 2002. Toxoplasmosis in three species of Hawaiian birds, nene goose (*Nesochen sandkensis*), Erckels francolin (*Francolinus erckelii*) and red-footed booby (*Sula sula*). J. Parasitol., in press.
- Work, T.M., Massey, J.G., Rideout, B.A., Gardiner, C.H., Ledig, D.B., Kwok, O.C.H., Dubey, J.P., 2000. Fatal toxoplasmosis in free-ranging endangered, 'Alala from Hawaii. J. Wildl. Dis. 36, 205–212.
- Yakimoff, W.L., Kohl-Yakimoff, N., 1912. *Toxoplasma canis* (Mello). Arch. Protistenk. 27, 195–206.
- Zhang, S.Y., Wei, M.X., Zhou, Z.Y., Yu, J.Y., Shi, X.Q., 2000. Prevalence of antibodies to *Toxoplasma gondii* in the sera of rare wildlife in the Shanghai Zoological Garden, People's Republic of China. Parasitol. Int. 49, 171–174.